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The Uptake of Nitrogen by Native and Agronomic Grasses

by



David Guy Paton

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH  
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE  
OF Master of Science

Department of Soil Science

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THE UNIVERSITY OF ALBERTA  
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The Uptake of Nitrogen by Native and Agronomic Grasses submitted by David Guy Paton in partial fulfilment of the requirements for the degree of Master of Science.





### Abstract

Three species of native grasses, alpine sheep fescue (*Festuca saximontana* Rydb.), Columbia needlegrass (*Stipa columbiana* Macoun) and slender wheatgrass (*Agropyron trachycaulum* (Link) Malte), and an agronomic grass, Magna smooth brome (*Bromus inermis* Leyss. cv. Magna), were used in ammonium and nitrate experiments to determine their uptake kinetics. The plants were grown in sand culture in a growth chamber and transferred to uptake solutions, using  $^{15}\text{N}$ , at various stages of their phenology. Most experiments dealt with the effects of plant age on nitrogen uptake, but other studies examined the effects of overcrowding, aeration and nutrient ions in uptake solutions, nitrogen deprivation and general growth characteristics.

The uptake data were interpreted according to Michaelis-Menten kinetics. Dual patterns of uptake were obtained for all four species of grasses for both ammonium and nitrate. It was found that the Michaelis constant,  $K_m$ , for ammonium uptake, was more or less independent of plant age, among all species, over the low range of concentration (0.0025 - 0.25 mM). These values varied between 0.014 and 0.039 mM. Over the high concentration range (0.25 - 5.0 mM), the  $K_m$ 's were higher and tended to decrease with age. For nitrate, the  $K_m$  values tended to increase over the low concentration range (0.001 - 0.75 mM) with increasing age and varied between 0.012 and 0.111 mM. Over the high





concentration range (0.75 - 10.0 mM), the  $K_m$  values tended to increase with age, and were much higher than  $K_m$ 's obtained over the low range. None of the grasses, whether native or agronomic, appeared to have any competitive advantage for extracting nitrogen at lower concentrations.

The maximum rate of uptake,  $V_{max}$ , was more species-dependent and varied more with external influences than  $K_m$ . With both ammonium and nitrate uptake, the  $V_{max}$  decreased with increasing age. The  $V_{max}$  was generally not significantly different between low and high concentrations. For example, the  $V_{max}$  of fescue decreased from 0.226 to 0.126 mg N taken up/g plant/2 h between 15 and 78 days over the low range of ammonium concentrations, while high range  $V_{max}$  values decreased from 0.399 to 0.338 mg N taken up/g plant/2 h.

All uptake experiments were conducted using  $(^{15}\text{NH}_4)_2\text{SO}_4$  and  $\text{Ca}(^{15}\text{NO}_3)_2$  in nutrient uptake solution which included  $\text{CaSO}_4$ ,  $\text{KH}_2\text{PO}_4$ ,  $\text{MgSO}_4$ , micronutrients and FeEDTA. There was no effect of these other competing ions on the uptake of ammonium.

All plants were starved of nitrogen prior to the uptake experiment. It was found that a 10 or 15 day starvation increased the uptake of nitrogen by 370 %.

It was found that there was no effect on  $K_m$  whether or not the uptake solutions were aerated. There may have been a slight effect on pre-treatment growing conditions where plants were raised in overcrowded pots.





A three compartment simulation model was developed using the experimental data to compare the relative differences in growth between the large, fast-growing agronomic grass, brome, and the small, slow-growing native grass, fescue. The model was driven by the production of carbon in the shoots, governed by plant age and shoot C/N ratios, and by the uptake of nitrogen by roots, controlled by root C/N ratio and external concentration. Portions of the newly assimilated carbon were translocated to the roots while all of the absorbed nitrogen in the roots was available for redistribution to the shoots.

The model was tested for validity against experimental dry weights and shoot/root ratios and for sensitivity by reducing the rooting volume and the external concentration of nitrogen. The model tended to underestimate plant nitrogen content over the first 60 days. It predicted that both brome and fescue would be subject to nitrogen stress under certain conditions; brome because it fully exploited the rooting volume and exhausted the soil nitrogen and fescue because it grew too slowly to build up adequate reserves of nitrogen. The model did not examine moisture stress or temperature effects, nor were losses of either nitrogen from the plant or internal nitrogen cycling considered.

The implications of the slower growth of some native grasses, are that in the first year, these plants may be less liable to exhaust soil nutrients than some of the





faster growing agronomic grasses. Thus, it may be more critical to fertilize the agronomic grasses than the native species. The model showed that fescue was more efficient in its uptake of nitrogen than brome and this competitive advantage would likely be manifested in succeeding years as the root mass of fescue increased in size.



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## I. Introduction

Field observations of dominance by bromegrass over mixed grass stands when nitrogen additions have been high, have led to the general assumption that bromegrass has a higher requirement for nitrogen than do many other grasses, especially the fescues. A corollary of this assumption is that some grasses grow well where there is little nitrogen available. If certain grasses tolerate low nitrogen levels or can remove nitrogen from soil at very low concentrations better than others, then they would be useful in reducing the need for nitrogen input into a system during reclamation. A competitive advantage in a nutrient-rich system often rests with the species capable of the fastest growth. Conversely a slow growth rate reduces demand on the environment and allows a species to make maximum use of a resource being supplied slowly. This concept of intensive or extensive demand applies to colonization of substrates by microbes and the fungal-bacterial interaction during decomposition, as well as competition between plants for a limiting nutrient or resource.

In soil-plant systems, both the above-mentioned factors of nutrient concentration and rates at which nutrients are converted from unavailable to available forms are important. Therefore the survival of a plant is related to the concentration below which it cannot remove nutrients and to the rate of supply of a particular nutrient.



In establishing this study, three basic assumptions were made. The first was that nitrogen was quantitatively the most important nutrient controlling plant growth, second that all other nutrients could be supplied to the plant in adequate amounts, and third that a suitable seed source could be developed which would enable the use of these species of grasses in reclamation schemes.

The objectives of this project were:

1. to review the literature for relevant information on methodologies, ion uptake by plants, nutrient supply in soil, models of nutrient cycling through soil-plant systems and strategies for the revegetation of disturbed lands;
2. to determine if the uptake of nitrogen was a function of species or external nitrogen concentration or both;
3. to measure the maximum rates of nitrogen absorption ( $V_{max}$ ) and the half saturation value or Michaelis constant ( $K_m$ ) by using solution culture and labelled ions of ammonium and nitrate;
4. to record dry weight production of shoots and roots and to obtain information on their growth characteristics in relation to nitrogen uptake;
5. to develop a simulation model as the first step in applying this data to field-grown plants to test the validity of the experimental values and their relationship to the growth characteristics of the individual species.



In the presentation of the various uptake experiments performed with these species, the general format for presentation of the data consists of an introduction, materials and methods and results and discussion for each experiment. The discussion is related to that particular experiment only. A concluding general discussion and summary section will integrate the individual sections. A simulation model will be presented to organize and graphically illustrate the relationships between kinetic parameters, plant growth and nitrogen uptake.





## II. Literature Review

### A. Introduction

In the following review, various ion uptake studies will be examined together with be some consideration of the possible mechanisms involved in ion uptake. Since the stable isotope of nitrogen was used in this study, there will be a brief review of the principles of isotopic research followed by some of the criteria for the selection of species that were used here. Movement of ions in the soil, various nutrition and reclamation studies, and some aspects of models of nutrient uptake and plant growth will conclude the review.

### B. Theory of Ion Uptake

The process of ion absorption and the sites of ion absorption have been studied extensively. The site of active transport of ions was proposed in the 1930's by the German plant physiologist Munch (1932 as cited in Bidwell, 1974), who introduced the terms apoplast and symplast. The apoplast consists of the apparent free space (AFS), the intercellular spaces and cell walls of the epidermal cells in the cortex of the root and tissues of the stele (mostly the xylem vessels). The apoplast is a discontinuous zone and the cells in the cortex of the root are separated from the stele by a

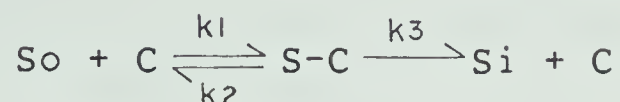


layer of suberized cell wall in the endodermis known as the Casparian Strip. This tissue prevents the passage of water through the AFS and forces it to cross the differentially permeable membrane or plasmalemma of the cell. The symplast consists of protoplasts or the portion of the cell within the plasmalemma. It is a continuous system, and the protoplasts of one cell are connected to those of another by thin canal-like plasmodesmata. Crafts and Broyer (1938 as cited in Bidwell, 1974) expanded the ideas of Munch and concluded that the symplast constitutes the site of active absorption. Ions are actively transported across the plasmalemma from the cortex, through the cell and then back across the membrane to the stele. This effectively raises the concentration in the stele while lowering it in the cortex. Later it was demonstrated by other workers (Bidwell, 1974) that the concentration of oxygen in the cortex region was sufficiently high to permit the metabolism necessary to generate the energy required for active transport. The fact that ions are accumulated far in excess of their concentration in solution around the root, is taken as evidence that this transport of ions into the stele is indeed active and not passive.

Epstein and Hagen (1952) applied the theory of Michaelis-Menten enzyme kinetics to the process of ion uptake. This theory states that substrate combines with a carrier to form a substrate-carrier complex. The complex transports the substrate across the cell membrane whereupon



the complex breaks down. It can be summarized as follows:



where:  $S_o$  = substrate outside the cell membrane

$S_i$  = substrate inside the cell membrane

$C$  = carrier

$S-C$  = substrate-carrier complex

The velocity of reaction as a function of substrate concentration can be represented as:

$$v = (V_{max})(S)/(K_m + S)$$

where  $V_{max} = k_3(S-C)$  when all the carrier is present as  $S-C$  complex and  $K_m = (k_2 + k_3)/k_1$  and takes a value of substrate concentration at which  $v = V_{max}/2$  (Cleland, 1970). The rate of reaction is directly proportional to the concentration of the substrate-carrier complex. At low values of  $S$ , the rate of reaction is proportional to  $S$ . At high values of  $S$ , the rate approaches a maximum velocity,  $V_{max}$  (Figure 1). From an interpretive standpoint,  $K_m$  is related to the efficiency of uptake. A lower  $K_m$  value signifies a greater affinity of the plant for that substrate such a plant would be more effective at extracting substrate from low concentration than a plant with a higher  $K_m$ . The maximum uptake rate,  $V_{max}$ , can roughly be taken as an index of the growth of the plant. A higher  $V_{max}$  in a given concentration range should produce a larger plant, or at least one with more nitrogen content than a plant with a lower  $V_{max}$ . However, the  $V_{max}$  value is subject to much more variation resulting from external influences such as temperature, light, pH, season, etc.





Calculation of the kinetic parameters  $K_m$  and  $V_{max}$  has traditionally been by graphical means. The Lineweaver and Burk (1934) method involves the plot of double reciprocals  $1/v$  versus  $1/S$  to obtain a straight line of slope  $K_m/V_{max}$  and intercept of  $1/V_{max}$  according to the following:

$$1/v = (K_m/V_{max})(1/S) + 1/V_{max}$$

The values derived from the lowest concentrations which should be the most susceptible to error, become the largest and therefore affect the final result to a large degree. While many studies have used the method of Lineweaver and Burk (1934), the preferred method in the present study will be that of Hofstee (1952). The uptake velocity  $v$  is graphed against  $v/S$  to obtain an intercept of  $V_{max}$  and slope of  $-K_m$  (Figure 2) according to the following:

$$\begin{aligned} v &= (V_{max})(S)/(K_m+S) \\ (v)(K_m+S) &= (V_{max})(S) \\ (v)(K_m) + (v)(S) &= (V_{max})(S) \\ (v)(S) &= (V_{max})(S) - (K_m)(v) \\ v &= V_{max} - (K_m)(v/S) \end{aligned}$$

The process of carrier-mediated ion transport generally is taken to follow Case I of Lineweaver and Burk (1934), where all the substrate-carrier complex is active, but it more closely resembles their Case VII, where:



In Case VII the rate of diffusion of  $S$  in the external medium to the point at which it can interact with the carrier  $S'$  is important and often the limiting factor in the overall reaction. Lineweaver and Burk (1934) thus



anticipated Nye (1977), who concluded that the rate of uptake of a nutrient may be limited by its rate of diffusion through the soil.

In any case, only the simplest form of Michaelis-Menten kinetics is applied to ion uptake by plants. Work by Fried *et al* (1965) and Epstein (1966) advanced the possibility that uptake was controlled by 2 or more mechanisms. The first was well-defined and was referred to as Mechanism 1, operating over a range of low concentrations and asymptotically approaching the theoretical parameter  $V_{max}$  at the high end of the concentration scale. Mechanism 2 was believed to operate at a higher concentration and often did not completely approach  $V_{max}$ . There were often several curves, which Hodges (1973) referred to as a "bumpy isotherm". Mechanism 1 appeared to be highly site-specific provided that calcium was present in the uptake solution; the results for Mechanism 2 did not appear to be as well defined. Mechanism 2 has also been claimed to be only the result of passive diffusion at high concentration (Barber, 1972).

Hodges (1973) postulated that the uptake mechanism was a single cation carrier and a single anion carrier, both with many different phases. He noted that the behaviour of the uptake parameters often appeared to follow pseudo-saturation behaviour (ie.  $K_m$  and  $V_{max}$  continually increased as substrate concentration increased). He incorporated the views of Koshland (1970) on cooperativity



kinetics of enzymes, and those of Eisenman (1961) on the changes in the selectivity of ions by cells with changes in external concentration. Hodges (1973) proposed a single multiphasic carrier which mediated ion transport. Koshland's (1970) model of an enzyme assumed it to be composed of many subunits, each possessing identical binding sites for a particular ligand or substrate. Ligand binding to the first subunit would induce a conformational change which distorted the other subunits sufficiently to alter their kinetic characteristics. In negative cooperativity, binding at one subunit by the first ligand would make it more difficult for the second to bind, thus resulting in an increase in  $K_m$ . Increasing ligand concentration would then approach a maximum more slowly, hence, the affinity of the subunits for substrate would decrease with an increase in ligand or substrate binding.

Eisenman (1961) showed that the sequences of transport selectivity of alkali cations changed with increasing external concentration. The basis of ion transport selectivity rests in the electrical field strength of the ion binding sites, and it increases as the external concentration increases. Hodges (1973) proposed that the conformational change in the subunits could lead to the change in field strength. This would account for the decreasing affinity for ions, or an increase in apparent  $K_m$ , as the external concentration increased.





The carrier-mediated process of ion transport is believed to be energy dependent and is more likely related to metabolism than transpiration (Rao and Rains, 1976; Sasakawa and Yamamoto, 1978). The energetics involved are rather complex and somewhat outside the scope of the present discussion. A good review is presented by Luttge and Higinbotham (1979).

### C. Nitrogen Uptake Studies

Numerous uptake studies have dealt with the alkali cations, some metals, phosphate and chloride ions. Relatively few studies have dealt with ammonium or nitrate ions. Nitrogen isotopes are stable and non-emitting (the emitting isotope,  $^{13}\text{N}$  has a half life of only 10 minutes and is not practical to use). The techniques needed to analyze the treated material using  $^{15}\text{N}$  are more time consuming than with other ions, which are emitting. The measurement of nitrogen ions from nutrient solutions into plants can be determined by the decrease in concentration in the solution or by analysis of the plant tissues following the uptake period. In the latter method, both labelled and unlabelled forms of nitrogen have been used, but it is preferable to use labelled ions for easier discrimination. There has been considerable debate as to whether or not there is more than one uptake mechanism, and therefore only the results that apply to Mechanism 1 (over a low concentration range) have



been used for comparative purposes (Table 1).

The  $K_m$  values for ammonium uptake ranged from 0.02 mM to 0.1 mM and for nitrate, 0.021 to 0.6 mM (Table 1). These values were determined from solution culture under standard conditions. They indicate that the  $K_m$  may fluctuate over a considerable range between various species of agronomic annual and perennial plants. However, it must be noted that rice for instance, may not have a well developed nitrate uptake system since it does not normally encounter nitrate in its growing conditions.

When conditions have been varied, considerable change in the kinetic parameters has been observed. Lycklama (1963) found that with ammonium uptake, the maximum rate of absorption,  $V_{max}$ , was dependent on temperature and accompanying anion. The Michaelis constant  $K_m$  was dependent upon seasonal factors (acclimation) but independent of temperature and accompanying anion. The optimum air temperature was between 22 and 27 C. The effect of pH was greater on seedlings than mature plants, with an increase in ammonium uptake with pH greater than 6.7; however this was again dependent on accompanying anion. With nitrate uptake the variations in the kinetic parameters were slightly different. The maximum absorption rate was dependent on root temperature, increasing as temperature was raised from 5 to 35 C.  $V_{max}$  was also dependent on pH with an optimum at 6.2 but was independent of the accompanying cation. Lycklama (1963) did not examine the influence of temperature and pH



on the Michaelis constant,  $K_m$ , but van den Honert and Hooymans (1955) suggested that it was independent of these influences.

Lycklama (1963) also found that while ammonium uptake was relatively unaffected by the presence of nitrate in the uptake solution, nitrate was greatly inhibited by the presence of ammonium. Fried *et al* (1965) found a similar relationship between the simultaneous uptake of ammonium and nitrate, even when the concentration of nitrate was far in excess of ammonium. High concentrations of rubidium, potassium and possibly calcium had some inhibitory effect on ammonium uptake. It is generally agreed that calcium should be present in the uptake solution, especially in the low concentration range (Epstein, 1972), and Rao and Rains (1976) found that nitrate absorption was increased as calcium was raised up to 5.0 mM.

The questions that Lycklama (1963) raised concerning temperature effects on ammonium and nitrate uptake have been studied actively in recent research. Their implications for kinetic studies are intriguing because it appears that the previous growing conditions to which the plant has become accustomed or acclimated may affect its performance in uptake experiments. Clarkson and Warner (1979) found that Italian ryegrass which had been grown at a temperature of 17 - 20 C exhibited greater ammonium absorption at both 20 C and 5 C, than plants grown at root temperatures of 8 C. Nitrate absorption was affected by low temperature to an





even greater extent. The critical temperature below which ammonium and nitrate absorption were markedly reduced was 10 C and 14 C respectively. Consequently the difference between ammonium and nitrate uptake was increased as the temperature was lowered. Their findings supported those of Sasakawa and Yamamoto (1978) who found that below 15 C nitrate uptake was negligible, while ammonium uptake was inhibited at 5 C.

One factor which did not appear to influence the Michaelis constant was age. It has been traditional to use young plants in uptake studies for a number of reasons, including ease of handling and the reduction in space needed to raise a large number of them. In young plants, the root is the only sink competing for nutrients; in older plants newly developing leaves, tillers and flowers can compete against the roots for nutrients. Fried *et al* (1965) used 14 day old rice roots and Rao and Rains (1976) used 6 day old barley seedlings. The maximum rate of absorption,  $V_{max}$  would be expected to increase as the mass of the plant increased (Edwards and Barber, 1976).

Warncke and Barber (1974) found that brome grass would absorb nitrate from concentrations as low as 1.5  $\mu M$ . Fried *et al* (1965) reported ammonium uptake from solution concentrations of 2.5  $\mu M$ , and Edwards and Barber (1976) reported that corn reduced nitrate levels to about 4.0  $\mu M$ . Warncke and Barber (1974) also stated that corn which developed symptoms of nitrogen deficiency, was growing in soil with levels of 40  $\mu M$  N, a concentration relatively



similar to the  $K_m$  value.

In agricultural soils, especially those which have been fertilized, levels of nitrogen as nitrate tend to be on the order of 0.1 - 10.0 mM. Nye and Tinker (1977, Table 3.1, p34). report the composition of various soil solutions. The values of nitrate ranged from 3.7 mM in cropped soils to 29.6 mM in fallowed land. In air dried samples of soils sampled near Ellerslie, Alberta, the 2 N KCl extractable nitrate content was 4.5 ppm. If this nitrogen were available in solution, the concentration would be about 1.0 mM (Norwest Soil Research Ltd., unpublished data).

It has been customary to use the Michaelis constant to compare the uptake properties of various plant species, but at high concentration levels it is  $V_{max}$  which determines uptake rate by the plant when the substrate levels are greatly in excess of the  $K_m$ . Normally substrate concentrations at the root surface are close to  $K_m$ .

#### D. Isotopic Research

The principles of the use of the stable isotope  $^{15}\text{N}$  have been outlined by Hauck and Bremner (1976). The main advantage of using a labelled source of nitrogen is that it provides a means of discriminating between sources of nitrogen and thereby reduces errors caused by difference methods. Because nitrogen is one of the main constituents of the plant, behind carbon, hydrogen and oxygen, the



quantitative difference between a small amount of recently assimilated N and a large amount of plant N cannot be accurately measured without a means of discrimination. Generally, if there has not been a labelled source of nitrogen used in an uptake study, the rate of nitrogen influx to the plant has been determined by the decrease in concentration of the uptake solution, although some studies have measured influx to the plant by analyzing the plant. However as Hauck and Bremner (1976) point out, there may be considerable difficulty in assigning an average background value to the plants.

There is some argument between researchers who have used a labelled source of nitrogen in the uptake study (Fried et al, 1965; Clarkson and Warner, 1979) and those who have measured the loss of N from solution (Lycklama, 1963; van den Honert and Hooymans, 1955 and 1961). For example Clarkson and Warner (1979) dispute the data of Lycklama (1963). They contend that his methods may show only a net flux of nitrate into the plant and may underestimate the actual influx of nitrate. In the present study, labelled forms of N were used in all uptake experiments.

#### E. Species Selection

When land is disturbed by overgrazing or mining, resulting in a loss of vegetative cover, one of the first concerns is replacement of that cover to prevent soil



erosion. For this purpose the use of grasses and legumes in initial revegetation schemes is preferred. The question of whether or not plants used in reclamation or rangeland revegetation should be agronomic or native species and if they should be in mixed or pure stands, has received considerable attention. Berg (1974) commented on the suitability of a large number of grasses and legumes for revegetation of subalpine areas in Colorado. While it may be intuitively sensible to select adapted native species, problems of seed availability and establishment on disturbed sites must also be considered. Berg (1974) cited smooth brome as an agronomic species which established well and was persistent in subalpine areas. Smooth brome has also been reported to dominate mixed stands, especially when fertilized heavily. Slender wheatgrass was also reported to establish well but was less persistent. In a later paper, Berg (1975) reported that the seedling vigour of slender wheatgrass was better than most native species. In Colorado, he reported that successful revegetation programs have largely been dominated by alfalfa and some of the taller grasses such as smooth brome and intermediate wheatgrass. However, Mayo (pers. comm.) suggests that some of Berg's (1974, 1975) observations, especially with regard to smooth brome and alfalfa, were contrary to his own.

Lesko *et al* (1975) investigating revegetation on coal mine spoils at Luscar, Alberta, found that wheatgrasses, smooth brome, timothy and junegrass were growing well after





two growing seasons. Monsen (1975) recommended that species used for reclamation should be ecologically adapted to a particular area. He observed that exotic or introduced species often afforded better protection to the soil initially, but tended to develop into monocultures which exhibited a decline in vigour with time. Selner and King (1977) found that in general, reseeded grasses survived better on undisturbed than disturbed sites. They attributed it to a better moisture regime in undisturbed ground [possibly also to a more well developed nutrient cycling system]. Selner and King (1977) observed that alpine sheep fescue tended to grow better on disturbed sites, but this was attributed to the slow growth and small size of fescue which would put it at a competitive disadvantage in an undisturbed site. Weaver (1919) also reported that fescue was slow growing and rather shallow rooted in relation to other species of the central grasslands in the United States. Wheatgrasses and brome grasses were considered to be deep rooting species.

Dormaar *et al* (1978) concluded that crested wheatgrass was a suitable alternative to native range on abandoned or marginal cropland in southern Alberta. However in stands of between 40 and 49 years of age, the crested wheatgrass had remained a monoculture and native species had invaded only to a limited extent. A study on interseeding (ie. seeding into an established vegetation cover) in North Dakota by Nyren *et al* (1978) concluded that production could be



increased substantially and a diversity of crops maintained when 5 species of grasses and 5 legumes were sown into 1 metre wide strips. They also found that tillage of the ground cover on either side of the interseeded area promoted water infiltration and did not increase the erosion hazard. They reported that a 60 cm wide tilled strip was most effective, as did Smoliak and Feldman (1978).

Ries *et al* (1978) concluded that the selection of grass species which established readily was essential to produce fully stocked initial stands for erosion control purposes. It appears that this approach, combined with interseeding at a later date, may be a better reclamation procedure than attempting to establish a diversity of slower growing plants at the outset.

There are several advantages attributed to native grasses over agronomic grasses according to Chapin (1980). He suggests that species from infertile habitats are generally slower growing as opposed to plants from more fertile sites which tend to exhibit rapid growth and acquisition of nutrients. The slow growth rate of some wild plants is less liable to exhaust soil nutrients. A rapidly growing species may suffer more physiological stress in a low nutrient system, resulting in a drastic reduction of dry matter yield, than a slower growing plant which may be more physiologically adapted to its nutrient-poor environment. A slow growth with some luxury consumption during nutrient flushes may be more beneficial than a rapid rate of growth



and overfeeding during flushes where rapidly accumulated levels of nutrients could lead to toxicity reactions (Chapin, 1980). The slower growing plants may be able to survive on their accumulated reserves longer than the faster growing species.

#### F. Nutrition and Reclamation Studies

Nutrition and reclamation studies conducted in the field and in the laboratory will be considered together in this section. The volume of literature which deals with the nutritional aspects of plant growth is extraordinary, and only a few papers have been summarized here. While it is well established that fertilizers enhance plant growth when they provide elements which are deficient, some of the specific responses of various plants are quite different.

Darrow (1939) studied the growth of Kentucky bluegrass in relation to nitrogen absorption temperature and pH. He found that bluegrass grew better when fed nitrate-nitrogen as opposed to ammonium-nitrogen. At a temperature of 15 C, there was a pH optimum of 6.5 for growth with ammonium, but between pH 4.5 and 6.5 there did not appear to be any optimum for growth with nitrate. Luxmoore and Millington (1971) studied the growth and nitrogen uptake of perennial ryegrass in relation to water content of the soil. They concluded that plants were unable to take up nitrogen at the rate at which it was conveyed to the plant roots.





The combination of nutrients used is also important. MacLeod *et al* (1971) found that root yields of rutabagas were increased by the application of nitrogen and potassium, but not by phosphorus applied singly. The yield response to nitrogen was also dependent on potassium supply. In early vegetative growth stages the nitrogen content in the tissues increased with increasing nitrogen application, but decreased with an increase in phosphorus or potassium. However in later growth stages, it was found that the accumulation of nitrogen was independent of phosphorus and potassium. Fitter and Bradshaw (1974) found that phosphorus increased the depth of root penetration and also the mass of roots in Italian wild rye. The correlation with the increases in fertilizer application was linear. At Grande Cache, Alberta, Macyk (1974) found that grasses responded better than legumes to applications of nitrogen. He used Magna smooth brome in spring seeding mixtures, with fertilizer rates of 110 kg N (as  $\text{NO}_3$ )/ha and 110 kg P (as  $\text{P}_2\text{O}_5$ ) and 90 kg K (as  $\text{K}_2\text{O}$ )/ha on a two year rotation. Nitrogen levels were depleted after this length of time without maintenance application.

Hamid (1972) examined the efficiency of nitrogen uptake by wheat using labelled fertilizer in field experiments. He found that wheat produced more dry matter if fertilized with nitrate-nitrogen. He concluded that N application increased the grain yield and quality. Several smaller applications of nitrate also were more effective than one large application



in the spring; this trend did not show up for ammonium fertilizer. Cox and Reisenhauer (1973) reported that wheat responded well to high levels of nitrate fertilizer if a small quantity of ammonium fertilizer was present. A similar relationship may apply to smooth brome which has been reported by various authors to dominate stands when fertilized heavily (Berg, 1974; Watson *et al*, 1980).

#### G. Movement of Ions in Soil

There are four main processes which supply ions or nutrients in soil to the root surface. The first one is contact exchange, a theory first advanced by Jenny and Overstreet (1938). It involved the direct transfer of an ion from a cation exchange site on the soil colloid to an exchange site on the root surface. The relative importance of this process is questioned by Barber (1962).

The second process of ion movement is diffusion. This involves the movement of an ion down a concentration gradient to the root surface. The gradient would be created by the active uptake of ions by the root. Diffusion is slow and must be considered as being of importance only over very small distances. Nye and Tinker (1977) reported a diffusion constant of chloride, which is very mobile in soil, of about  $10^{-5}$  cm<sup>2</sup>/sec. Diffusion may become relatively important as the moisture content of the soil decreases although this changes diffusion rate because of tortuosity.



The third process is mass flow. Nutrients dissolved in the soil water, are drawn towards the plant. This process has also been termed solvent-drag, and would be of greatest importance when the soil moisture content is at or near the field capacity and when the concentration of nutrients is high. Nye and Tinker (1977) state that water flux to a root rarely exceeds  $5 \times 10^{-6}$  cm/sec or 0.4 cm/day. There are a number of controls on the movement of ions in soil and these were summarized by Barber (1962) as follows:

1. initial concentration of the ion in the soil;
2. rate of ion uptake per unit of root surface;
3. rate of diffusion of ions to the root;
4. rate of movement of ions by mass flow and;
5. capacity of the soil to replenish the solution ions.

Another mechanism of delivery not considered by all workers, is root extension. It has been shown that the rate of growth of young roots may be in excess of 1 mm per hour (Yoneyama *et al*, 1975), which is considerably greater than the rate of diffusion and at least as great as the rate of mass flow. Caldwell (1976) used a rate of 2 cm/day in his model of root extension and water absorption. Weaver (1925 as cited in Kramer, 1969) found that grass roots commonly grow at rates of 1.25 cm/day and the principal vertical roots of corn could grow downwards at maximum rates of 5 - 6 cm/day for three or four weeks.

Most of the work on ion movement and root growth in soil remains in a fairly theoretical state, since the actual



measurements involved to test these theories are extremely difficult and time consuming. The initial concentration of ions in soil solution can be measured, but is usually reported on an average moisture content rather than at specific intervals of moisture content (Carter, 1977). The rate of ion uptake can be measured from solution culture and extrapolated to soil situations. The rate of replenishment of ions in soil has been examined in decomposition studies using labelled isotopes. However the total picture of ion movement in relation to plant growth remains somewhat obscure due in large part to the heterogeneous nature of soil even at the micro-scale at which plant roots absorb nutrients.

#### H. Nutrient Cycling and Modelling

In a native grassland, the nitrate levels are low, normally less than 1  $\mu\text{g}$  N/g soil while ammonium concentrations of 5 - 10  $\mu\text{g}$  N/g soil are more common (Soulides and Clark, 1958). Paul (1977) states that this results in low losses of nitrogen within the system since most of the nitrogen is in ammonium form or immobilized in plant and microbial biomass. Approximately 60% of the net annual productivity of grasslands may be ascribed to below-ground parts (Clark, 1975). When combined with the high productivity of microorganisms, there is an annual below-ground standing crop which is about 10 times the





productivity of the above-ground portions. Yet the amount of quantitative information for below-ground systems is very small. Traditionally, fertilizer applications have been correlated with above-ground crop yield only. Models dealing with nutrient fluxes in soil have used approximate values and will have to continue to do so for some time until their use stimulates enough detailed research to provide more exact experimental data. Singh and Coleman (1974) found that 62% of the total root biomass in a shortgrass prairie to 60 cm depth was functional. But Clark (1974) working in the same prairie, concluded that only 36% of the roots were functional. Part of this discrepancy results from differences in sampling time and definition of a functional root.

Clark *et al* (1975) conducted experiments on the early uptake of labelled nitrate-nitrogen in a shortgrass prairie. They sampled at periods of 2 hours and 14 days after application of the  $^{15}\text{N}$ . They found that the litter component of the system (above-ground dead, senescent and detrital roots) accounted for 67% of the labelled nitrogen immobilized 2 hours after application. This was believed to be due partly to absorption and partly to immobilization by microorganisms. At the end of 14 days, green tops and crowns had accumulated 72% of the added nitrogen, giving firm evidence of active uptake. Live roots contained 7%, and the litter the remainder. This distribution of nitrogen was not affected by application rate. Thus it can be seen that



regardless of the percentage of functional roots, or the amount of N applied up to a point, uptake of fertilizer nitrogen is rapid. After 2 years, 80% of this nitrogen was still in the plants either in living tissue or in dead or senescent roots.

The living and dead plant residues represent a significant proportion of the nitrogen budget of the soil-plant system. Paul (1977) stated that grassland plants may contain up to 20% of the nitrogen in the system, of which about 13% may be found in the roots. The plant residue component of the grassland system represents one of the most dynamic components of this system according to Campbell *et al* (1976). The turnover rate of N in plant residue, living and dead in chernozemic soils, was estimated at 2.5/y, which corresponded to a half life of only 4 months. Microbial biomass was the next most dynamic component with a half life of 1.2 years. However one may suppose that nitrogen cycling within the microbial population alone would be considerably greater. The microbes control the nitrogen cycle and any nitrogen cycled is processed by them. Campbell *et al* (1976) presented a model for the turnover of nitrogen and the loss of N from agricultural soils following cultivation. They used the turnover rates mentioned for plant residues and microbial biomass and also considered mineral N, relatively labile organic and stable organic nitrogen components. Although as stated earlier, the plant residue component accounts for the fastest turnover rates, there may be a



greater total amount of N cycled through the slow moving humus component due to its large size. The amount of various forms of soil organic N and their turnover rate controls the rate of supply of N to plants. This N passes through the soil solution to the root and it is this root surface - soil solution - soil solid interface that links the supply rate of nutrients and their concentration to the survival of the plant community which we observe above the soil surface.

Models of nutrient cycling or nutrient absorption within a system provide a framework in which to integrate a large number of concepts, observations and experimental data in a concise manner. The operation of the model will often direct the course of future research so that the greatest benefit can be achieved with a minimum of repetition. Models may point out trends in the data which would have been overlooked otherwise. The use of modelling procedures is expanding, but unfortunately much of the information available was collected without the original intention of using it in this manner. Therefore much of this data has been of limited value.

Brewster and Tinker (1970) modelled nutrient flows of cations around plant roots by diffusion. In their first approximation, they considered that the root behaved like a cylindrical absorber and that there were no influences from plant exudates, mycorrhizae or large pH changes which might affect uptake. Drew and Nye (1969) concluded that root hairs should also be included in the root model. Evidence from





autoradiographic studies showed that there were large zones of depletion around the roots which could not be explained by diffusion alone. It was believed that the root hairs increased the volume of soil that could be exploited by a single root. Later papers such as Baldwin *et al* (1972, 1973) examined the spatial arrangement and density of roots in finite volumes of soil.

The movement of solutes in the soil-root system has been studied extensively by Nye and Tinker (1977). Their treatment involves the simultaneous processes of mass flow and diffusion. From a calculation of flux of ions into the plant a relative growth rate may be obtained and total dry matter production may be inferred. It is important to stress that Nye and Tinker (1977) and their associates have been concerned with the uptake of nutrients on a micro-scale rather than on a larger scale such as by a whole plant. Their unit of length is 1 cm and the unit of time is 1 second. Therefore when they calculate the flux of a nutrient ion into the plant, it may be on the scale of pmol/cm/s. When researchers such as Fried *et al* (1965) or Lycklama (1963) report kinetic parameters, they do so on the basis of mol/g plant/h. What they are actually measuring according to Nye and Tinker (1977) is an average  $K_m$  and  $V_{max}$  based on the sum of many uptake velocities from over the entire root system. For this reason it is difficult to compare data where the time and size scales are not the same.



Reuss and Innis (1977) proposed a nitrogen flow model for grasslands. The model consists of simple production and decomposition submodels, with soil water and temperature as driving variables. The basic soil system and values for variables are entered into the model, which was compartmented into 8 partitions with a total of 23 state variables in the nitrogen flow section. In the live root uptake of nitrogen, only the uptake of nitrate-nitrogen was considered. Ammonium was considered to be completely oxidized to nitrate. The absorption of nitrate was considered to follow typical Michaelis-Menten kinetics and was described as the sum of two processes, each with a maximum rate  $M$ , and a half saturation constant  $K$ . The velocity or uptake rate,  $U$ , in  $\text{mg N/g root/d}$ , was controlled by substrate concentration  $S$ , in  $\text{g N/m}^3$ , such that:

$$U = (M_a)(S)/(K_a+S) + (M_b)(S)/(K_b+S)$$

where:  $M_a = 2.0 \text{ mg N/g root/d}$

$M_b = 0.4 \text{ mg N/g root/d}$

$K_a = 84 \text{ g N/m}^3$

$K_b = 4.8 \text{ g N/m}^3$

Kinetic parameters were not actually measured, but are consistent with the observed behaviour of the system. The values  $M_b$  and  $K_b$  would be associated with Mechanism 1 of Epstein (1966) operating over a low concentration range;  $M_a$  and  $K_a$  would be associated with Mechanism 2 at a higher range of concentration. The model resulted in an accumulation of nitrate in the roots so a reverse flow mechanism was built into the model to decrease net nitrate



uptake at high levels. Reuss and Innis (1977) explain that the absorption of ammonium was more difficult to simulate because of soil effects, such as cation exchange, fixation in clays, etc. and make a case for the collection of more relevant data concerning grasslands.

By its very nature a model has to be a simplified representation of the system it is simulating. Several assumptions may be questioned in the model of Reuss and Innis (1977). One of these is that only the absorption of nitrate has been considered. While this may be valid, there is an ammonium component, and it would have to be nitrified at a very high rate in order that all of the ammonium be unavailable for uptake by plants. Nitrate uptake has been simulated according to a dual pattern of uptake, whereas the actual validity of the second mechanism operating over a high range may be questionable. In the present study, where the uptake rates of ammonium and nitrate are being determined for various native and agronomic grasses, the values obtained could be substituted directly into the model of Reuss and Innis (1977).

McGill *et al* (1981) have developed a grassland simulation model that includes both C and N cycling and overcomes many of the conceptual problems in the Reuss and Innis (1977) model. Plant components considered are living roots, living shoots and standing dead matter. Litter (dead organisms) is divided into a rapidly recycling N-rich metabolic component and a structural component which



decomposes slowly. The microbial component considers both bacteria and fungi. This model treats plant uptake of both ammonium and nitrate nitrogen. Unique features include concurrent mineralization and immobilization of N, population density effects on decomposition when the substrate is also the habitat, density-dependent death of microorganisms, the manner in which litter is partitioned which implies faster internal recycling of N than of C, a cascading system of soil organic matter cycling and the high degree of interaction between plants and microorganisms. The model does not, however, treat  $N_2$  fixation very mechanistically and does not handle plant establishment from seed.

A different analytical model, designed for the utilization of nitrogen, phosphorus and potassium has been proposed by Smith (1976). Ion transport to the plant root was modelled on the basis of mass flow and diffusion, and element uptake was modelled on the carrier theory (Michaelis-Menten kinetics). The model predicted first order responses to any combination of macronutrients over a wide range of plant species. The model showed that much of the deficient responses of plants to N, P and K could be explained as linear responses to low concentrations and toxic responses as inhibition by N, P and K at high nutrient levels. The model confirmed the Liebig Law of the Minimum and also demonstrated that the Liebig theory of linear growth in response to nutrient concentration, and the





non-linear Mitscherlich Law of Diminishing Return are not necessarily in opposition, but may apply to different parts of the concentration range. Models of this type help to confirm or refine current concepts about the supply and utilization of nitrogen by the soil-plant system.

This literature review has attempted to integrate some of the pertinent information about the soil-plant system. The need for more quantitative information and more importantly the need for the information to be collected within the framework of an existing model so that the correct parameters are measured is apparent. With increased knowledge about the kinetic activities of the grassland system, a more effective effort can be made towards its reclamation and its long term stability.



### III. General Materials and Methods

#### A. Introduction

In the following discussion, the procedures used in the preparation and treatment of samples will be reviewed. Subsequent experiments will refer to this 'General Materials and Methods' section and only mention new methods that apply to that particular experiment. This section is divided into two parts, the first dealing with the actual selection and growth of the grasses, and the second with the analytical methods used in the experiments and the manipulation of data.

#### B. Plant Growth Materials and Methods

##### Species Selection

The selection of species of grasses was made on the basis of several criteria including range and habitat, apparent rate of growth, response to fertilizer, use or consideration in reclamation programs and potential availability of a reliable seed source. Textbooks and classification manuals such as Moss (1959), Hitchcock (1935) and Hulten (1968) were consulted to determine the range, habitat and growth characteristics of the grasses considered. The suitability of various species in reclamation trials and rooting characteristics were



reviewed. The seeds were obtained from Dr. David Walker, Dept. of Genetics. The three native species chosen were those which, in his opinion, had a promising potential for reclamation work.

1. Magna smooth brome - (*Bromus inermis* Leyss. cv. Magna). Magna brome is an agronomic grass which is available commercially. It has been widely used in reclamation schemes (Macyk 1974) and in highway ditch revegetation (Yarish, personal communication). It is a fast growing grass, particularly at high levels of fertilizer application. Berg (1974) mentioned that when brome is fertilized intensively it often dominates the site and this aspect was deemed to warrant further investigation. Bromegrasses in general are deep-rooted and rhizomatous.
2. Alpine sheep fescue - (*Festuca saximontana* Rydb.). This is a native bunchgrass of the prairies and foothills. In Alberta, fescue tends to grow best in the moister Black and Dark Brown Soil Zones of the prairies. It has been observed to grow well at low fertilizer levels and is known to be rather shallow rooted (Weaver, 1919). It was also suspected to be rather slow growing. The seed originated from plants collected on Mount Rae (batch #132) by Dr. D. Walker.
3. Columbia needlegrass - (*Stipa columbiana* Macoun). This native grass has the most limited range of all the native species used. It is restricted to the prairies and foothills of southern and southwestern Alberta and





the interior of British Columbia and south into the United States. Needlegrass is a deeprooted, fairly fast growing, robust and hardy grass. This seed was collected from ecotypes on Pigeon Mountain.

4. Slender wheatgrass - (*Agropyron trachycaulum* (Link) Malte). This wheatgrass occurs throughout the prairies and foothills region. It is a deep-rooted grass of drier meadows and alkaline environments and is considered to be drought-hardy and salt-tolerant. According to Walker *et al* (1977) this species shows great promise for reclamation work. Dewey (1960) reported that slender wheatgrass had a high salt tolerance index, but that germination was reduced by salinity stress. The original source of the seed was ecotypes on Gibraltar Mountain (batch #104).

#### Growth Medium

The grasses were grown in fine washed sand. According to Matkin *et al* (1957), sand in the size range of 0.1 to 0.5 mm is well suited to sand culture and has fair water holding capacity. FG-3 sand, purchased locally from Sil Silica Ltd., met these size criteria (Table 2). Particle size distribution was determined by sonic sifter (Table A-1 of the Appendices).

#### Containers

The plants were grown in free-draining 18 cm plastic pots. Approximately 2 cm of pebble-size gravel and 1 cm of



number 3 granite grit was placed in the bottoms of the pots before the sand was added. This was found to be an effective barrier preventing the loss of the fine sand, while permitting free drainage and, consequently, aeration.

### Planting Method

Prior to planting, all pots were saturated and allowed to drain freely for about 1/2 hour. A planting jig was used to make holes 1 cm deep for the wheatgrass, brome and needlegrass. Holes 0.5 cm deep were used for the smaller fescue seeds. Two seeds were placed in each hole and covered with dry sand. The pots were then covered with black plastic sheeting and seeds were allowed to germinate (approximately 1 week to 10 days). Plant population was reduced to 5 plants per pot after emergence.

### Environmental Conditions

The plants were grown in a growth chamber. The day-length was 16 hours and the day-time temperature was 20 C. The night-time temperature was lowered to 15 C. The relative humidity was about 55% during the day but rose to about 90% during the night. The illumination provided by a bank of 2.4 m cool white fluorescent tubes was approximately 20,000 lux at a vertical distance of 2.5 m from the plants. No incandescent lamps were used.



## Nutrient Solutions

Nutrients were provided by watering with a nutrient solution, prepared after comparing different formulae listed by Hewitt (1966). The total nitrogen content was kept low (112 ppm), less than a modified Hoagland's solution (Johnson *et al*, 1957 in Table 3)(196 ppm), and was similar to the formula used by Shive and Robbins (1942). Both nitrate and ammonium were present and the  $\text{NO}_3/\text{NH}_4$  ratio was 4.0 (Table 3). Iron was added as the chelated compound ferrous dihydrogen ethylenediamine tetraacetic acid (FeEDTA) (Table 4). For each litre of nutrient solution, 0.5 ml 1.0 N NaOH was used to raise the pH to 5.9. The macronutrient compounds used were:  $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ ,  $\text{KH}_2\text{PO}_4$ ,  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$  and  $(\text{NH}_4)_2\text{SO}_4$  in a ratio of 4:3:2:1.

The plants were watered in excess with the nutrient solution when the water content of the sand dropped to 50% of the available water. Prior to the uptake experiment the plants were starved of nitrogen for a period of 10 days for the faster growing wheatgrass and brome and 14 days for the slower growing needlegrass and fescue. The purpose of the starvation period was to ensure that a maximum rate of uptake would be attained during the experiment. The nitrogen-free solution was composed of  $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ,  $\text{KH}_2\text{PO}_4$ ,  $\text{MgSO}_4$ , micronutrients and FeEDTA, in ratios of 2:3:2:1:1. The N - free nutrient solution has a higher sulfate concentration and a lower calcium concentration due to balancing of compounds (Table 5). The pH was adjusted to 5.9



using 0.4 ml/l 1.0 N NaOH.

### Germination of Seed

Initially the wheatgrass failed to germinate. Several different methods of planting and pre-treatment of seeds were used with variable and often inconsistent results. The preferred method of seeding was to plant directly into a pot at field capacity (after draining 1/2 hour). It was found that draining and drying of the sand for 3 to 4 days before seeding, resulted in approximately 90% germination success, but test pots kept constantly moist and regularly watered prior to emergence also produced high germination figures. When the pots were allowed to dry out only 1 day prior to planting, germination success was 46%. When the wheatgrass seeds were soaked in several changes of distilled water for 6 hours prior to planting in a pot at field capacity, and kept moist, the germination percentage rose somewhat, but was still rather variable, fluctuating between 55 and 80%.

### Miscellaneous Problems

Another problem associated with the use of sand culture and nutrient solution was the growth of algae on the surface of the sand. Initially to combat this problem, styrofoam beads were used to cover the surface of the sand. These beads were messy and difficult to handle. It was also observed, that when plants became infected by aphids, some of the aphids appeared to be living among the styrofoam





beads and thus were relatively unaffected by spraying with Malathion. The algae did not appear to adversely affect plant growth, but these pots required more solution during watering to saturate the sand, and the rate of water loss was greater from algae covered pots than styrofoam bead covered pots. In lieu of the styrofoam beads, number 3 granite grit was used, and this appeared to be quite satisfactory in controlling algae. Aphids continued to be a problem and were sprayed with pesticide for control.

### C. Analytical Materials and Methods

#### Nitrogen Uptake Experiments

The duration of the uptake experiment was 2 hours and was similar to the method of Fried *et al* (1965). Single plants were washed out of the sand cultures and transferred to uptake solutions (Tables B-1 and B-2, Appendices), one plant per one litre container. Three replicates were used for each of 14 dilutions of  $(^{15}\text{NH}_4)_2\text{SO}_4$ . The concentrations ranged from 2.5, 5.0, 7.5  $\mu\text{M}$ , 0.01, 0.025, 0.05, 0.075  $\text{mM}$ , and so on, to 5.0  $\text{mM}$  (10.0  $\text{mM}$  for nitrate). It was expected that this would be sufficiently wide to cover both a low and a high concentration range of ammonium absorption. An aeration system consisting of aquarium valves and airstones provided both aeration and mixing of the solutions during the uptake period.



## Analytical Methods

The particle size distribution, bulk density, porosity, hydraulic conductivity, and Kjeldahl analyses were performed as outlined in McKeague (1978). Following their exposure to labelled N in the uptake solutions, the plants were rinsed twice in distilled water and placed in individual paper envelopes to dry. Plant samples were dried at 65 C for three days and then weighed to determine root and shoot dry matter weights using an analytical balance. The entire plant sample was then finely ground and stored in plastic containers. For total N analysis approximately 0.1 grams of sample were used in duplicate analysis with 7 ml of Kjeldahl acid. During the distillation process, 30 ml of 10 N NaOH was used. The ammonia was collected in 4% boric acid and titrated with 0.1 N  $H_2SO_4$ . Following the determination of total N, an additional 1 ml of titration acid was added to further acidify the samples. The samples were reduced in volume to about 3 or 4 ml following titration and were stored in a cool place in 1 dram vials until analysed on the mass spectrometer. Later, samples were evaporated to dryness. Mass spectrometer analysis yielded the percent abundance of  $^{15}N$  which was used to calculate the percentage of the total nitrogen in the plant which was  $^{15}N$ , all of which came from the uptake solution (Table C-3, Appendices).

In order to facilitate the processing of a greater number of samples at one time, a digestion block was constructed, modelled on a Tecator unit. Two blocks of



aluminum 38 cm x 38 cm were bolted together. One block was 5 cm thick and was drilled with 40 holes, 2.65 cm (ID) in a 5 x 8 grid 22.5 cm x 17.5 cm. The lower plate, 2.5 cm thick was left unmarked and a small quantity of sand was placed in the bottom of each hole to better distribute the heat. If a single block of aluminum is used, 7.5 cm. thick, the sand would not be necessary as the bottoms of the holes would be already bevelled from the action of the drill bit. The block was insulated with 2.5 cm of kaowool board and was covered in galvanized iron to protect the soft insulation. The digestion block was mounted on a hot plate, with the top cover of the plate removed so that the block rested on the asbestos strips, leaving a small space between heater elements and block. This apparatus was hooked up to a relay which was activated by a simple electric timer. It was found that 4 hours on high heat were required for complete digestion, of which approximately 2 hours were required to bring the Kjeldahl mixture up to boiling. The maximum temperature attained was near 320 C depending on the condition of the heater elements. The tubes used in this block were made locally using 25 mm (OD) glass tubing, 36 cm. in length (75 ml total volume to mark on constriction), with a constriction of 3 cm., 30 cm. from the base. It was found that up to 10 ml of Kjeldahl mixture could be used in the tubes, but when more than this was used, there was some loss during boiling. The efficiency of the N digestion and steam distillation method was about 95% for standard total





nitrogen methods, and about 90% if a nitrate pre-treatment was used, as outlined in McKeague (1978).

#### Tabular Data

The results have been expressed on a per gram of plant basis. Three sets of data have been presented in the tables of uptake data (Tables 9, 10, 12, 13 and 14), corresponding to the low concentration range (2.5  $\mu\text{M}$  - 0.25 mM), high concentration range (0.25 - 5.0 mM), and the corrected values for the high range of concentrations which have been calculated by subtracting the low range values from the high range values. This calculation is necessary to fully delineate the two mechanisms responsible for uptake. However, since mechanism 2, which operates over the high range of concentration, is subject to controversy, the discussion will mainly be concerned with the low concentration range values corresponding to mechanism 1. The units for  $V_{\text{max}}$  are mg N taken up/g plant/2 h. The Michaelis constant,  $K_m$ , is expressed in millimolar (mM) concentration. The coefficient of determination ( $r^2$ ) is presented along with the number of the means in parentheses over which the regression was run. In the uptake experiments there were 14 concentrations or treatments with either 3 replicates or 6 replicates for each treatment. Young plants at 15 - 17 days of age were not large enough to permit duplicate analysis. The first mean (Number 1) corresponds to the lowest concentration, 2.5  $\mu\text{M}$   $\text{NH}_4$ , while the fourteenth corresponds



to the highest concentration, 5.0 mM  $\text{NH}_4$ . Some of the ranges of means associated with the coefficient of determination indicate that a mean was not included in the regression (eg. .86 (9-14,-13) indicates a value of  $r^2$  of .86 over the means of treatments 9-14 with number 13 excluded). A mean would be excluded from the regression when it varied considerably from the other means. For example, means 1, 2, 3, and 4 are far to the right and were excluded (Figure 4). For most of the data, 95% confidence intervals (eg.  $.226 \pm .035$ ) have been constructed. A difference in significance between two numbers was based on the overlap of the confidence intervals.

### Graphical Data

Some sample graphs showing the break in the data are presented in Figures 3 and 4. The raw data in tabular form and statistical summaries of the three measured parameters - weight of sample, total nitrogen content and percent excess  $^{15}\text{N}$  - are presented in the Appendices (sections D -K). The regression constants for  $V_{\text{max}}$  and  $K_m$  were determined using an APL program for simple linear regression located in APL Public Library 2, Statpack 2, but the lines plotted on the graphs in Figures 3 and 4 are not regression lines but trend lines fitted visually. The form of the plot used to determine the kinetic parameters was the Hofstee (1952) transformation which plots uptake velocity,  $v$ , on the y-axis, against uptake velocity divided by substrate



concentration,  $v/S$ , on the x-axis. The y-intercept becomes the  $V_{\max}$  value; the slope of the line is  $-K_m$ . The calculation used to get uptake velocity  $v$  is (% excess  $^{15}\text{N}$  in plant / % excess  $^{15}\text{N}$  in solution)  $\times$  total %N in plant converted to mg N/g plant.



## IV. Observations on Plant Growth

### A. Introduction

The main objective of this study was to obtain data concerning the uptake kinetic behaviour of three native and one agronomic species of grasses and to assess their relative usefulness in reclamation work. This included the observation of these plants as they grew and collection of quantitative information on plant weights, nitrogen contents and phenology.

### B. Plant Weight and Nitrogen Content

Samples were taken at various ages for all the grasses to determine root and shoot weight. Some of these samples were also analyzed for nitrogen content. Most of this sampling was conducted on plants grown at a population of 15 plants per pot. There was very little sampling done later when plants were grown at 5/pot, but qualitative observation suggested that the plants grown at the lower rate were healthier and larger for some species. This will be discussed in more detail in the next section. The data shown in Table 6 are mean values, generally derived from harvesting one pot of 15 plants. The pots of plants which appeared to be in the best condition were reserved for uptake experiments, while the remainder were harvested. This





resulted in a deterioration of the quality of the dry weight measurements. It was also found that it was very difficult to completely remove the sand grains from the roots, especially in brome and fescue. This led to inaccuracies in root weights. Generally, dry weights were not taken after it was decided to grow plants at a density of 5 plants per pot, since that decision tripled the number of pots required to produce the 42 plants needed for each uptake experiment.

A separate study devoted solely to obtaining growth parameters such as dry weight, root length and leaf area index would provide valuable baseline data on the growth of these species. An exhaustive literature review might also yield similar results or at least data which could be extrapolated to the present study. When graphed, the data for all species indicate that growth followed an S - shaped curve with an early period of exponential growth, followed by a decline in growth and levelling out. This trend was particularly evident in needlegrass. Similar graphs can be found in the section dealing with the validation of the simulation model.

The total nitrogen content showed a gradual decline but was variable and poorly defined (Table 7). The average nitrogen contents of brome and fescue were essentially the same, at 3.55% and 3.52% respectively; the average N contents of wheatgrass and needlegrass were 3.18% and 3.05%, respectively.



### C. Qualitative Observations on Plant Growth

By 140 days of growth, fescue still had not rooted to the bottom of the pot; most of the roots were within 8 cm of the surface. The fescue roots were very fine with no secondary branching and very few root hairs. The root mass was light brown in colour and very dense. Fescue top growth was very slow but leaves were plentiful in relation to its size. By day 72, the maximum leaf length was 15 cm, there was no discernible stem and there were 450 leaves per plant. Fescue did not flower although some plants were grown as long as 150 days. Dr. D. Walker (pers. comm.) suggested that fescue required a cold dormancy period to stimulate flowering.

Needlegrass grew more rapidly than fescue but slower than brome, and did not need staking for support. The leaves were curled or boat-shaped and even mature plants stood straight and tall. This was in contrast to both brome and wheatgrass which were staked at an early age (day 30-40). The roots of needlegrass were light brown in colour and showed both main and secondary roots and rootlets. Main roots extended to the bottom (18 cm) of the pots and had a moderate covering of root hairs.

Wheatgrass was a fast-growing grass with leaf growth to 60 cm. None of the wheatgrass flowered or produced heads in 90 days. The wheatgrass was particularly weak stemmed at 15 plants per pot but at 5 plants per pot this characteristic was not so evident. The roots of wheatgrass extended to the



bottom of the pots (18 cm), were white with both main and secondary roots and a moderate covering of root hairs. In a completely different study examining its nitrogen and phosphorus nutrition, it was discovered that wheatgrass was susceptible to iron deficiency and the amount of iron added as FeEDTA had to be doubled to prevent chlorosis at later stages of growth. It was also found that the germination of wheatgrass seed was inconsistent and often unpredictable.

Brome was a fast-growing grass, and grew extremely rapidly when seeded at 5 per pot. At maturity the culms exceeded 1 metre in height. The leaves were flat and wide. The root mass was dark brown in colour with main and secondary branches densely covered with root hairs. This grass sent out several tillers which added to its above-ground production. Brome generally produced heads by 60 days and flowered by 80 days.

When the plants were grown at a density of 15 per pot, they were extremely difficult to remove from the pots after 80 days of growth due to interwining and entanglement of the root mass. When grown in less-crowded conditions at 5 per pot, the root masses were separated with relative ease. Fescue with its very fine root mass, and the brome with its dense covering of root hairs both tended to accumulate sand particles which were exceedingly hard to remove without damaging the root. This is a desirable attribute from the standpoint of initial surface stabilization.





During the pre-uptake starvation period, both wheatgrass and brome exhibited nitrogen deficiency as indicated by a lighter green colour. However, neither fescue, nor needlegrass, exhibited any gross symptoms of nitrogen deficiency during starvation periods.



## V. The Effects of Aeration and Pre-treatment Conditions on the Uptake of Ammonium

### A. Introduction

The first seven uptake experiments were conducted without the benefits of an aeration system in the uptake solution. The plants were grown at 15 per pot, and it was felt that the removal of the plants from the sand may have resulted in some damage to the roots. In most experiments, the plants were grown at 5 plants per pot and there was an aeration system in the uptake solutions. Epstein (1972) suggested that the effect of aeration was twofold. First it provided a source of oxygen during the experiment and second, it provided a means of stirring the solutions thereby preventing the formation of any zones of depletion. Some research (cited by Epstein, 1972), indicated that the level of oxygen needed to attain maximal uptake rate was only 2%. The objective of the present experiment was to examine the effects of crowding on  $V_{max}$  and the lack of an aeration system on  $K_m$ .

### B. Materials and Methods

The same species were used as outlined in 'General Materials and Methods'. The plants were grown at 15 per pot and instead of gravel in the bottom, paper towels were used.



The uptake experiment was conducted as outlined in 'General Materials and Methods' except that there was no aeration of the solutions.

## C. Results and Discussion

### Effect on Plant Size

The physical size of the plants grown at 15 plants per pot appeared to be less than those grown at 5 per pot (Table 8). The growth data shown for 5 plants per pot were derived for the most part from uptake experiments, where the plants had been deprived of N prior to the experiment. The differences were most striking in brome, but there was little difference with fescue or needlegrass.

### Effect on Km

Results have been given for 6 uptake experiments only (Table 9), although 7 were originally conducted. The uptake experiment for brome at 39 days is shown in Table D-13 in the Appendices. It was the first uptake experiment to be performed in this study, but there was no trend in the data at all. It was difficult to say if there was a net uptake or a decrease over the two hour period. It is not known why this occurred, since subsequent experiments were carried out under the same conditions and techniques.

The confidence limits for Km are rather wide, suggesting variability in mixing and its subsequent



influence on diffusion and uptake (Table 9). When the  $K_m$  values obtained over the low concentration range were compared to data which examined the effect of age on uptake for fescue (Table 12, Figure 5), it was found that the  $K_m$  value at 50 and 99 days under the conditions described above, were not significantly different from the value obtained in age experiments for seedlings or full-grown plants, although the  $K_m$  values for plants grown at 15 per pot and not aerated were slightly higher at both ages than the  $K_m$  values for fescue grown at 5 plants per pot and aerated during the uptake period. Over the high range of concentrations there were no significant differences in  $K_m$  and there were no apparent trends in the data (Table 9, Figure 6). The results here tend to support the argument that the  $K_m$  value remains constant with age.

For needlegrass, there were no significant differences in the  $K_m$  values over the low range of concentrations (Figure 5), although there was a trend to increase with age. Over the high range, the  $K_m$  values at 15 plants per pot and not aerated, were less than and significantly different to the  $K_m$  values obtained at 5 plants per pot and aerated (Figure 6).

For wheatgrass there was only one non-aerated experiment. There were no significant differences in the  $K_m$  values over both concentration ranges between aerated and non-aerated experiments (Figures 5 and 6).





In the case of brome, the non-aerated experiment was conducted at 87 days. The  $K_m$  values were similar over both concentration ranges (Figures 5 and 6). There did not appear to be any effect of lack of aeration or mixing on the  $K_m$  values.

The data presented in Table 9 agreed with those obtained under conditions of aeration and less crowding. Therefore, it was concluded that there was very little effect of competition or of lack of aeration on the ability of these species to take up nitrogen. However it must be pointed out that the plants that were grown under more crowded conditions were subject to periodic moisture stress, especially at older ages, even when the period between watering was only 1 or 2 days.

It was also very difficult to remove the older plants from their pots at 15 plants per pot because the roots were incredibly tangled, especially brome and wheatgrass, and there was possibly some root damage caused by the removal from sand. The uptake experiment for wheatgrass at 88 days was omitted because the roots were too tangled to separate, and the uptake experiment for brome at 87 days was extended over 2 days to allow time to wash out the roots. But this does not appear to have influenced their ability to absorb ammonium.

Effect on  $V_{max}$



For fescue, over both concentration ranges, the  $V_{max}$  values for non-aerated plants grown at a density of 15 per pot were significantly lower than  $V_{max}$  values for plants grown at 5 per pot and aerated during uptake (Figures 7 and 8). It is probable that the overcrowding prior to the uptake experiment had a greater effect on  $V_{max}$  than aeration or stirring during the uptake experiment. To some extent this reduction was reflected in growth as the 78 day old plants, grown at 5 per pot, weighed more than 99 day old plants grown at 15 plants per pot (Table 8). This would suggest that fescue does not react well to crowded conditions, an observation consistent with that of Selner and King (1977).

For needlegrass, the maximum uptake rate was less for overcrowded plants than plants grown at a lower seeding density over both concentration ranges (Figures 7 and 8). At the lower concentration range, only the  $V_{max}$  value of the crowded plants at 87 days was significantly lower but over the high range, all  $V_{max}$  values were significantly lower.

The  $V_{max}$  values of wheatgrass grown at 15 plants per pot were significantly different from those grown at 5 plants per pot over both concentration ranges (Figures 7 and 8). A similar relationship applied to brome.

On the basis of this experiment, it was concluded that there may have been some effect on  $V_{max}$  by overcrowding, resulting in a decrease in  $V_{max}$ . It appears to be better defined in the case of fescue, which was the smallest of the four species used here, but was also a bunchgrass, whereas



the other three grasses all produce tillers to varying degrees. In these three species, the reduction in  $V_{max}$  could be attributed to age alone.

#### D. Summary

This experiment demonstrated that there were no deleterious effects on  $K_m$  caused either by pretreatment crowded growing conditions or by a lack of aeration in the uptake solution. In this case, one litre containers were used. There must have been sufficient oxygen in the solutions to permit energy mediated transport processes in the root over a 2 hour period. Further no apparent zones of depletion developed around the roots during the uptake period, because if there had been, there would have been an overall increase in the apparent  $K_m$  due to diffusional effects. Such an increase was not observed. The effect of crowding on growth may have been reflected in lower  $V_{max}$  values but the trends are uncertain.

It was concluded that growing plants at 5 per pot was essential in this type of work to eliminate logistical problems at later growth stages and to minimize competition effects on the plants. Aeration was not shown to be critical but its inclusion in future uptake studies is recommended and was followed throughout the rest of this study.



## VI. The Effect of Other Ions in the Ammonium Uptake Solution

### A. Introduction

The purpose of this experiment was to examine the effects of the presence of other cations and anions in the ammonium uptake solution on  $K_m$  and  $V_{max}$  of fescue. Inhibition of ammonium uptake by potassium has been reported for rice (Fried *et al*, 1965). The ions present in the nutrient solution were calcium, potassium, magnesium, phosphate and sulfate, as well as a suite of micronutrients and iron as FeEDTA as listed in Table 4, with varying concentrations of labelled  $(^{15}\text{NH}_4)_2\text{SO}_4$ . The reasoning behind the use of the nutrient uptake solution was that it approximated the composition of a soil solution. The control was labelled ammonium sulfate in distilled water.

### B. Materials and Methods

Fescue was grown for 78 days at 5 plants per pot. Single plants were transferred to aerated uptake solution. Standard conditions as outlined in 'General Materials and Methods' were employed throughout.





### C. Results and Discussion

There was no significant effect caused by competing nutrients on the Michaelis constants,  $K_m$ , or the maximum rates of uptake,  $V_{max}$ , over either concentration ranges (Table 10). Although there were no significant differences in  $V_{max}$ , there was a tendency for  $V_{max}$  to be slightly reduced in the treatments without nutrient ions. Fried *et al* (1965) reported less than 30% inhibition by rubidium, potassium and possibly calcium, on the uptake of ammonium, even if these complementary ions were present in tenfold higher concentrations.

It would seem that the  $K_m$  measured from a solution containing only the labelled ion would not be representative of a soil system. A Malmo SiCL at a water content of 30% had a soil solution of the following composition - calcium, 7.2 mM; magnesium, 2.3 mM; potassium, 13.2 mM and sulfate 0.5 mM (Norwest Soil Research Ltd., unpublished data). The nutrient solution used in the uptake experiments was roughly equivalent to Malmo soil solution but had higher levels of sulfate and phosphate (Table 3). Nye and Tinker (1977) list soil solutions of comparable composition. Consequently,  $K_m$  values reported on the basis of uptake from solutions containing only the labelled ion, should be examined very carefully. In many of the reported experiments it is not made clear what the actual composition of the uptake solution is. Fried *et al* (1965) describe it only as "the appropriate solution". They do not specifically state



whether labelled ammonium sulfate was added to the dilute culture solution or to distilled water. Rao and Rains (1976) included calcium as well as chloride, bromide and sulfate in their solutions. Sasakawa and Yamamoto (1978) apparently used solutions containing only the labelled ions. Lycklama (1963) used a dilute culture solution similar in composition to the one used in the present study, but at much reduced levels. It has been generally agreed that calcium must be included in the uptake solution, in order to preserve the integrity and selectivity of the differentially permeable membrane (Epstein, 1972).

#### D. Summary

Uptake experiments were performed throughout this study using nutrient solutions rather than distilled water to permit interpretations on the basis of soil conditions. It is noteworthy that the extent of the difference in  $K_m$  caused by competing cations is small. It was concluded that there was no effect of other ions in the uptake solution on the kinetic uptake of ammonium by fescue. Further these findings appeared to be of a general nature and were assumed to hold for all the species used in this study.



## VII. The Effect of Pre-Treatment Nitrogen Starvation on the Uptake of Ammonium by Brome

### A. Introduction

The objective of this experiment was to determine if N uptake rates were affected by N content of the plant. Plants may accumulate N through luxury consumption following fertilization (Viets, 1965), but yet use of N slows down after most needs have been met. There are, however, no data available to relate relative uptake rate to N content of the plant. It was decided to assess the effect of this treatment on brome which was the largest and fastest growing of the plant species used.

### B. Materials and Methods

Brome was grown at 5 plants per pot under standard conditions to 61 days with starvation periods of 0, 5, 10 and 15 days prior to the termination of growth. During this period the plants were watered with N-free nutrient solution (Table 5). At the end of 61 days, the plants were washed out of the sand and single plants were placed in containers of nutrient solution containing 0.1 mM  $(^{15}\text{NH}_4)_2\text{SO}_4$  at 31.3% excess  $^{15}\text{N}$ . Approximately 14 samples were used at each starvation level and the samples were analyzed in duplicate for total N and  $^{15}\text{N}$  content.



### C. Results and Discussion

There were no significant differences in plant due to starvation (Table 11), but the overall trend was to a reduction in plant weight with increasing starvation period. Nitrogen starvation reduced the amount of N taken up by the plant by 12%, 26% and 42% during 5, 10 and 15 days of starvation respectively. Utilization of its stored N reserves may account for reduced N contents without significantly affecting plant weight.

The  $^{15}\text{N}$  contents of the brome increased with starvation periods, by 203%, 361% and 381% for 5, 10 and 15 days of starvation respectively. Due to the similarity between the  $^{15}\text{N}$  contents at 10 or 15 day starvation periods, it was surmized that at this point, the plants were taking up nitrogen from solution at their maximum rates.

The % excess  $^{15}\text{N}$  content was taken as an index of uptake. When expressed on a per g plant basis relative to the highest ratio at 15 days, the relative uptake rates were 0.91, 0.47 and 0.23 mg N taken up/g plant/2 h for 10, 5 and 0 days of starvation respectively (Table 11). Similarly the relative uptake rate of N/g plant N/2 h was 0.72, 0.31 and 0.14 for starvation periods of 10, 5 and 0 days respectively.





#### D. Summary

From the results of this experiment, it has been possible to establish a relationship between N content of brome plants and their N uptake rate. Such a relationship is essential to understand N uptake following fertilization and is expected to be reasonably fundamental and therefore general.

This experiment confirmed the idea that a starvation period would enhance the uptake of nitrogen. Although it was only tested on brome at 61 days with ammonium uptake, the same relationship was assumed to apply to nitrate uptake and ammonium uptake for all species at all ages. The length of starvation prior to subsequent uptake experiments was 14 days for the larger plants and 7 days for the seedlings.



## VIII. The Effect of Age on the Uptake Rates of Ammonium by Grasses.

### A. Introduction

Three species of native grasses and one agronomic grass were examined for their ability to take up ammonium over a wide concentration range at two different ages. Edwards and Barber (1976) reported that the Michaelis constants of both ammonium and nitrate were essentially the same in corn and showed no significant variation with plant ages between 15 and 58 days. They also found that the maximum rate of absorption decreased with age. The highest values of maximum rate occurred with 15 - 24 day old plants. Lycklama (1963) used full-grown plants and seedlings (13 days) in his experiments. He found that full-grown plants had a  $K_m$  of 0.04 mM at between 20 C and 35 C but seedlings had a  $K_m$  of 0.1 mM at 25 C. The seedlings were grown in the greenhouse, however, while the full-grown plants were obtained from the field. Therefore, Lycklama (1963) did not attempt to correlate age with uptake rates under controlled conditions.

### B. Materials and Methods

The four species of grasses mentioned in the previous section were used in aerated uptake experiments of 2 hours duration. There were 3 replicates for each of 14



concentration levels. For the plants at 15 days, the analyzed sample consisted of the entire plant, but for the older plants, there was sufficient sample to allow duplicate analyses. The means of the treatments were used in the regression analysis for determination of the kinetic parameters. Over the low concentration range the means most commonly used were treatments 2-8 or 2-9 while for the high range, means 9-14 or 10-14 were used. This represented concentration ranges of 0.005-0.1 or 0.005-0.25 mM and 0.25-5.0 or 0.5 - 5.0 mM.

### C. Results and Discussion

There appears to be two mechanisms which control uptake (Table 12), one operating over a high concentration range and one over a low concentration range. According to Hodges (1973) and Epstein (1972) there may or may not be a valid mechanism operating over the high range of concentration, and in fact, experiments over higher ranges of concentration seem to indicate a "bumpy" concentration line or "pseudosaturation" behaviour. If in fact this is the case, then only the data collected over the low concentration range can be readily compared to other studies. The generally accepted range of the low concentration is 0.005 - 1.0 mM (Epstein, 1972; Cox and Reisenhauer, 1973). Statistically, there were significant differences in  $K_m$  between values obtained over corrected high and low



concentrations at the same age for all the species, but generally not for  $V_{max}$ .

### Trends Within Species

In fescue,  $K_m$  decreased slightly between 15 and 78 days (Figure 9), though not significantly, in the low concentration range. Over the high concentration range, there was no significant difference between  $K_m$  values (Figure 10), although the  $K_m$  at 15 days was greater than that at 78 days. Therefore it was concluded that there would not be a loss of affinity for ammonium by the roots of fescue with an increase in age. The decrease with age in maximum rate of uptake,  $V_{max}$  (Figures 11 and 12), was significant only at the low concentration range (Table 12).

The  $K_m$  values were not significantly different with increasing age for needlegrass over high or low concentration ranges (Figures 9 and 10). The  $V_{max}$  decreased by factors of 2 and 4 times over low and high concentration ranges respectively and was significant (Figures 11 and 12).

For wheatgrass, there were no significant differences in  $K_m$  values within the low or high ranges with increasing plant age (Table 12, Figures 9 and 10). The  $V_{max}$  values tend to decrease in wheatgrass by factors of about 9 times over high and low concentration ranges between 15 and 78 days (Figures 11 and 12).

The  $K_m$  value increased slightly with age (Table 12) in brome over the high concentration range but  $K_m$  values were





not significantly different between 15 and 78 days for either concentration range (Figures 9 and 10). The maximum rate of absorption decreased by factors of 9 and 5 times between 15 and 78 days over low and high concentration ranges (Figures 11 and 12). Brome did produce heads by about 60 days and this could have had an effect on  $V_{max}$  as well.

### Trends Between Species

Over both concentration ranges, there were no significant differences in  $K_m$  between the species at either 15 or 78 days (Figures 9 and 10). Thus, it appears that plants may be rather similar in their ability to extract ammonium from the soil solution. The retention of this ability with increasing age does not appear to be species dependent.

The maximum uptake rates for seedlings over the low concentration range (Figure 11), show that the order of increasing uptake rate is needlegrass < fescue < wheatgrass = brome. For 78 day old plants the order was wheatgrass < brome = needlegrass < fescue. Over the high concentration range (Figure 12), there was no difference in  $V_{max}$  at 15 days but at 78 days, the order was wheatgrass < needlegrass = brome < fescue.

While all species exhibited a reduction in  $V_{max}$  with increasing age, by day 78, the maximum uptake rate of fescue remained high and exceeded the rates of all other species. There was very little effect on  $K_m$  with increasing age



though, and this would appear to contradict Chapin (1980) who stated that plants from infertile habitats may have a lower  $K_m$  and also a generally lower  $V_{max}$ . Fescue appears to have developed an efficient system for the uptake of ammonium.

Brome was the only grass used which produced flowers, although needlegrass was very close to this stage. The effect that flowering may have had on  $V_{max}$  is unknown, but the reduction in  $V_{max}$  with age is similar in wheatgrass which did not flower.

The values of  $K_m$  obtained for ammonium uptake over the low range of concentration at the seedling and full-grown stage compare well to those values obtained for other plants (Table 1). Edwards and Barber (1976) reported that corn exhibited  $K_m$  values between 0.018 and 0.027 mM between 15 and 58 days, with no significant differences being shown in any of the data. It appears that generally the  $K_m$  value falls within the range 0.013 - 0.1 mM and that with increasing plant age this range is constant.

As mentioned previously, the kinetic values for the high range of concentration are thought to be representative of pseudo-saturation kinetics rather than true Michaelis-Menten kinetics.  $K_m$  values in the high concentration ranges (0.162 - 1.32 mM), were slightly lower than the value obtained by Fried *et al* (1965) for rice roots (3.0 mM).



#### D. Summary

The following conclusions can be drawn about the four species used here with respect to age and ammonium uptake.

1. The  $V_{max}$  tended to decrease with age, especially in wheatgrass and brome at both concentration ranges.
2. The  $K_m$  values over the low range appear to be between 0.014 - 0.039 mM, are not significantly different and are independent of age for the species used here.
3. There is a tendency for the  $K_m$  value to increase with age in faster growing species and decrease in slower growing species over the high concentration range.
4. Fescue had one of the lowest uptake rates at 15 days but the highest at 78 days.



## IX. The Effect of Age on Uptake of Nitrate by Grasses

### A. Introduction

The purpose of this experiment was to examine the effect of age on the uptake of nitrate. Edwards and Barber (1976) suggested that  $K_m$  was independent of age, and Fried *et al* (1965) indirectly suggested that a dual uptake pattern for nitrate may exist.

### B. Materials and Methods

The same species were used as in 'General Materials and Methods'. The uptake solutions were aerated in the same manner. The uptake experiments were conducted using plants of similar age to those used in the ammonium uptake experiments (15 and 78 days), but the plants used here varied from 15 to 17 days and 78 to 84 days. Three replicates per treatment were used in the uptake experiments with seedlings and older plants. The older plant samples were analyzed in duplicate for total N content with a pre-digestion treatment for nitrate as outlined in McKeague (1978). The uptake solution concentrations were somewhat different, starting at 5.0  $\mu$ M and extending to 10.0 mM. The means of the treatments at each concentration were used in regression analysis to determine the kinetic parameters. All of the confidence intervals were calculated at the 95% level





unless otherwise noted. The means used to determine the high range values were generally 10 or 11 to 14, corresponding to the range 0.75 - 10.0 or 1.0 - 10.0 mM, while the means used to determine the low range were generally 4 - 10, corresponding to 0.025 - 0.75 mM. It was found that the first 3 means, 0.005, 0.0075 and 0.01 mM generally displayed inconsistent uptake patterns and so were eliminated from most plots. Fried *et al* (1965) used a similar concentration range to that reported here but found that the lower limit of their detection of uptake was about 0.05 mM.

## C. Results and Discussion

### Trends Within Species

There was no significant difference in  $K_m$  with age over high or low ranges of concentration in fescue (Table 13, Figures 13 and 14). The values for  $V_{max}$  decreased with plant age over both concentration ranges (Figures 15 and 16). The  $V_{max}$  values are not significantly different between high and low ranges at 79 days of age, but the  $K_m$  values for fescue are significantly different between high and low ranges.

With needlegrass there was no difference in  $K_m$  value with respect to age at the high range (Figure 14), but there was significant increase in  $K_m$  value in the low range (Figure 13). The  $V_{max}$  decreased by a factor of about 3 times between 15 and 84 days over both high and low ranges (Figures 15 and 16).



The  $K_m$  values for wheatgrass were significantly different between 17 and 79 days over the low range of concentration (Table 13) and increased by a factor of about 9 times (Figure 13). Over the high range of concentrations there was a non-significant increase in  $K_m$  with age (Figure 14). The  $V_{max}$  decreased significantly with increasing age for high and low ranges respectively (Figures 15 and 16).

With brome, the  $K_m$  in the low range increased between 15 and 80 days, though not significantly (Figure 13). The  $K_m$  in the high range was not significantly different with increasing age (Figure 14). The  $V_{max}$  values for the brome seedlings decreased with age by factors of 10 and 6 for low and high ranges respectively (Figures 15 and 16).

### Trends Between Species

The values of the Michaelis constant,  $K_m$ , over both concentration ranges were not significantly different for the plants at the seedling stage (Figures 13 and 14). At 79 days the pattern was fescue=brome<needlegrass=wheatgrass, over the low range. There were no significant differences in the  $K_m$  values over the high range at 79 days, although the order of increasing  $K_m$  was fescue=brome<needlegrass<wheatgrass. Wheatgrass tended to have a lower affinity for nitrate at increasing age over both concentration ranges, but the other species were similar in their ability to extract nitrate. Fescue being a native range plant, has developed under conditions of low



nitrate concentration typical of such systems (Soulides and Clark, 1958). It appears to have developed an efficient system to utilize the low concentrations available, whereas other native grasses, such as needlegrass and wheatgrass, appeared to lose some of their ability to extract nitrate with increasing age. The affinity of brome for nitrate is relatively independent of age.

The maximum rate of uptake over the low concentration range was the same for seedlings and the decrease with age was similar between species (Figures 15 and 16). Over the high concentration range, the  $V_{max}$  values for seedlings at 16 days showed that the decrease for fescue was less than the other 3 species and at 79 days, while there was not a significant difference, the  $V_{max}$  values of fescue and brome were similar and less than those of needlegrass and wheatgrass. Although brome produced heads by at least 60 days, the reduction in  $V_{max}$  with time was similar to other species which did not flower.

The data reported in Table 13, generally agreed with previously reported data (Table 1), where only the lower concentration range values have been reported. Edwards and Barber (1976) found that there was no significant difference between  $K_m$  values for corn between 15 and 58 days of age. Their values ranged from 0.018 to 0.027 mM. Generally that trend was found in the present study within species, but as pointed out earlier,  $K_m$  can be seen to increase with age in some of the species. The  $K_m$  values, averaged between young



and old plants, were 0.015, 0.056, 0.064 and 0.026 mM for fescue, needlegrass, wheatgrass and brome respectively. Fried *et al* (1965) reported a  $K_m$  value of 0.6 mM for excised rice roots; this was reduced from the original level reported because of ammonium inhibition. However the method used by Fried *et al* (1965) did not appear to be as sensitive as that used in the present study, as nitrate absorption was found to occur at a lower concentration than they were able to detect. Their use of rice which normally does not have access to nitrate may be an important factor here. Rao and Rains (1976) found a  $K_m$  value for barley seedlings of 0.11 mM, which is closer to the values reported here.

#### D. Summary

The following conclusions can be drawn about the four species used here with respect to age and nitrate uptake.

1. All species exhibited a dual pattern of nitrate uptake.
2. The maximum uptake rates decreased with age over both ranges of concentration. All four species had  $V_{max}$  values of similar magnitude between 16 and 79 days over the low concentration range.
3. At the seedling stage 15-17 days, there were no differences in  $K_m$  values among the species over either low or high concentration ranges. However there was a tendency for needlegrass and especially wheatgrass to lose some efficiency of nitrate uptake with increasing





age (ie. higher  $K_m$  values with age).

4. Over the low concentration range, the  $K_m$  values of seedlings are in the range 0.012-0.024 mM but by 79 days this increased to 0.111 mM (wheatgrass) and 0.99 mM (needlegrass).
5. There was no indication that the agronomic grass, brome, had a competitive advantage with respect to nitrate uptake.



## X. The Translocation of Ammonium and Nitrate into Shoots of Brome

### A. Introduction

During the analysis of brome plants following nitrate and ammonium uptake experiments, the shoots were separated and analyzed apart from the roots. The purpose of this experiment was to examine the distribution of absorbed nitrogen between roots and shoots so that an estimate of nitrogen translocation could be obtained.

### B. Materials and Methods

Brome was used in uptake experiments at age 78 and 80 days for ammonium and nitrate respectively. The conditions under which the plants were raised and the experiment conducted have already been outlined in previous ammonium and nitrate uptake sections. The data given in those two sections for mature brome plants were derived from the joint data of roots and shoots combined, and the weighted averages of the root and shoot weights were used to determine the relative proportions of each component to generate the data for the entire plant. The kinetic parameters were determined in the usual manner. It was found that often there was less variance for the values calculated for the entire plant rather than the measured data for roots or shoots



separately. The data for the whole plant tended to follow those obtained for the roots, while the shoots were sometimes quite different.

### C. Results and Discussion

The trends in the data for ammonium and nitrate uptake were similar over the low concentration range. There were no significant differences between  $K_m$ 's for roots or shoots with ammonium or nitrate uptake, although the  $K_m$  values for shoots tended to be lower (Table 14). The  $V_{max}$  values for shoots were significantly lower for both ammonium and nitrate uptake. The  $V_{max}$  for root uptake of ammonium was significantly higher than the  $V_{max}$  of root uptake of nitrate.

Over the high concentration range, there were no significant differences between  $K_m$  values for shoots or roots, although the confidence intervals obtained for  $K_m$  values are rather wide. There was a significant difference between the  $V_{max}$  of root uptake of ammonium compared to the shoot uptake. There was no difference in the  $V_{max}$  data of roots or shoots and nitrate uptake over the high concentration range.

From the uptake data obtained, it was possible to calculate the relative proportions of nitrate-N and ammonium-N being translocated from the roots to the shoots over a 2 hr period. The results of these calculations showed



that about 25% of the total amount of ammonium-N absorbed was translocated to the shoots (Table 15). There was an decrease in the proportion of ammonium-N translocated with increasing concentration. On the average, about 54% of the nitrate-N absorbed by the roots was translocated to the shoots within two hours. There was more absorbed nitrate than ammonium translocated at every concentration. The amount of absorbed nitrate translocated was more or less constant with increasing external concentration. Brome had a higher maximum uptake rate for ammonium than nitrate, though.

There was approximately twice as much nitrate moved into the shoots as ammonium. Yoneyama *et al* (1975) examined nitrogen transport in corn and found a lag of 8 minutes for ammonium and 4 minutes for nitrate between absorption at the root tip and appearance in the basal tissue. They concluded that the main reason for this was that ammonium first had to be converted to amino acids and amides before before it was transported, while nitrate was transported directly.

#### D. Summary

From this experiment it was concluded that nitrate was more mobile in the plant than ammonium and that significant amounts of the nitrogen taken up over the 2 hour experimental period were translocated from the roots to the shoots. This relationship probably applies to other grasses





as well and was assumed to be general.



## XI. A Model of Nitrogen Uptake and Plant Growth

### A. Introduction

For the purpose of summarizing and organizing all of the data collected in this study, a simulation model was constructed to better delineate the relationships between nitrogen uptake and plant growth. The constants used were obtained from the experimental data in this study, with plants growing from seed to 120 days old, or approximately the first growing season. The model was run using the IBM simulation language CSMP III (Continuous Systems Modelling Program). The plant was divided into 3 compartments, the shoot, old root growth and new root growth. There are several basic assumptions inherent in the model.

1. Michaelis-Menten kinetics operating over the low concentration range controlled the uptake of nitrogen.
2. N uptake was a function of root length per unit volume of soil exploited.
3. Nitrate and ammonium were both present and totally in solution. Their concentrations were reduced only by plant uptake and nitrification of ammonium.
4. Uptake was an active process which occurred only in daylight, 16 hours/day for 120 days.
5. The growth of roots into new zones of solution concentration was the most important process by which nutrients were brought to the root surface.



6. Ammonium and nitrate were both taken up and ammonium did not inhibit the uptake of nitrate.
7. The plants were not stressed, either through temperature, aeration, moisture or nutrient supply effects, excluding nitrogen.

The two species used were brome and fescue. These two grasses are completely opposite in growth form and habit. Brome was very large, fast growing, with wide flat leaves and fescue was small, slow growing, with narrow thin leaves.

It was envisaged that there were two variables controlling plant growth - photosynthesis and nitrogen uptake. Photosynthesis was restricted to the shoot compartment and at each hourly iteration of the model a portion of the newly assimilated carbon was translocated to the roots. Photosynthesis was controlled by age and the shoot carbon to nitrogen (C/N) ratio. A maximum rate of growth was calculated which applied only to the shoot between Day 0 and Day 15. The relative shoot growth rate was adjusted to decrease with increasing plant age, and increasing shoot C/N ratio. The uptake of nitrogen was restricted to the root compartment and was based on the experimentally derived  $V_{max}$  and  $K_m$ . A relative uptake rate of N was adjusted with respect to root C/N ratios.

A copy of the computer program of the simulation model is presented in Section M of the Appendices.



## B. Mathematical and Theoretical Basis

### Kinetic Parameters

The kinetic parameters had already been determined from the uptake experiments and these were inserted directly into the model. The  $K_m$  values were more or less constant with increasing age so only an average  $K_m$  value was used. For brome, the  $K_m$  value for ammonium was 0.0412 mM and for nitrate, 0.0257 mM. For fescue the values used were 0.0435 mM and 0.0150 mM for ammonium and nitrate respectively. The maximum value for  $V_{max}$  that was measured from the experimental data occurred at the seedling stage (about 15 days old). These values were used in the model as constants. The experimental units were mg N taken up/g plant/2 hr, and these were converted to mol N taken up/g plant/hr by dividing the experimental  $V_{max}$  value by 28,000.

### Shoot Growth Rate

A maximum shoot growth rate was calculated from seed weight at time zero and the first measured dry weight at about 15 days. The maximum shoot growth rate, MGR, was calculated as follows:

$$(dW/dt)(1/W) = MGR = (\ln W_1 - \ln W_0)(1/dt)$$

where:  $t$  = time

$W_1$  = weight at time 1

$W_0$  =  $W_t$  at time 0

$dW$  = change in weight

$dt$  = change of time

The units of MGR were  $h^{-1}$ . Because the growth rate thus





calculated was for the whole plant, it was multiplied by 2 to be representative of shoot growth.

### Carbon Translocation

There is almost no pertinent literature which examines carbon translocation over a single growing season for grasses. Much research has been conducted on carbon translocation in legumes, but few researchers have examined grasses, due in part, to the problem of tillering. With a legume there is one root and one shoot, but many grasses have more than one above-ground shoot, which makes the interpretation of results sometimes rather difficult. Several studies have dealt with a single pulse of  $^{14}\text{C}$  at a single point in the life cycle of a grass, generally later in its growth, after flowering. This literature was considered to be of little value to the present study.

In earlier versions of this simulation model, carbon translocation values were obtained from a grassland nitrogen cycling model (McGill *et al*, 1981). Specifically, the translocation data used was for blue gramma grass. They envisaged that approximately 70% of the recently assimilated carbon would be translocated to roots by 10 days, and eventually 100% by 100 days. This data were not compatible with the present model. Nyahoza *et al* (1974) worked with Kentucky bluegrass at 42 days and found that between 12.5 - 17.5% of the carbon was translocated to roots from various tillers. Similarly St. Pierre and Wright (1972) found that



at the 3 leaf stage, timothy translocated 50% of its carbon to the lower shoot, roots and new tillers, and by the 5 leaf stage, the rate was about 17%. Some data on lupines by Withers and Forde (1979) indicated that carbon translocation may be rather constant with increasing age. They found that 21%, 18.4% and 18.6% of the recently photosynthesized carbon was moved to the roots at 2, 50 and 110 days respectively.

In the present simulation model the amounts of carbon translocated were calculated from dry weight data (Table 6). For example, brome at day 26 had a shoot/root ratio of 0.73 (ie. 0.73 g shoot/ 1.00 g root). Since all of the carbon was assumed to originate in the shoot and be transported only one way to the roots, this would represent 0.73 g C retained in the shoot and 1.00 g C translocated to the root. In other words 57.8% of the carbon was translocated to the roots (Table 16). At day 34, the change in total plant weight was 0.24 g and the change in root weight 0.08 g, indicating 33% of the shoot carbon was translocated to the root. Similarly, by comparing changes in root weight and total plant weight, translocation rates of 18.2% by day 74 and 15.3% by day 82 were calculated (Table 16). The data was graphed using the midpoints of the time intervals, and slightly modified prior to use in the simulation model. The data indicate a steady rate of carbon translocation of 57.8% between day 0 and 26, but a rate of 40% at day 0 was used to get a more suitable simulated total weight and shoot/root ratio. The rate of translocation was held constant between 79 and 110 days at



15.3% but was increased to 100% translocated at 120 days. The reason for the 100% translocation at 120 days was to reduce the shoot/root ratios, limit growth and simulate death of shoots, although it is not known whether there is physiological data to support this viewpoint. Similarly, values for carbon translocation were calculated for fescue (Table 16).

### Relative Growth Rates

The growth rate with respect to age was calculated for brome and fescue from dry weights (Table 6), using the equation  $\text{Growth Rate} = (\text{d}W/\text{d}t)(1/W)$ , and converting to a percentage of the maximum (Table 17). The midpoints of the time intervals were used in these data.

The data for the change in shoot growth rate with respect to the shoot C/N ratio was obtained from McGill *et al*, (1981) from a grassland simulation model. It was used for both fescue and brome. The relative growth rate was 100% when the shoot C/N ratio was between 0 and 18. The rate was decreased to 90% of the original (maximum shoot growth rate, MGR) at C/N 24, 60% at C/N 35 and 0% at C/N 50.

### Relative Uptake Rate of Nitrogen

The uptake rate of nitrogen with respect to root C/N ratio was calculated from the brome starvation experiment (Table 11). The C/N ratio was calculated from the total weight and nitrogen content, assuming 45% as the carbon



content, on a weight/weight basis. The amount of labelled  $^{15}\text{N}$  taken up was used as an index of uptake rate, and this was converted to uptake rate/g plant (Table 11), and expressed as a percentage of the highest rate at 15 days of starvation. It was thought that the uptake of N would be an ongoing process and thus the relative rate was held at 0.23 for root C/N ratios between 0 and 13.8. Similarly at high root C/N ratios (greater than 23.7) the relative rate was 1.0. The starvation experiment examined brome only, but in the simulation model relative rates were applied to fescue as well.

#### Root Extension

From values reported in the literature and already discussed, the rate of root elongation was much greater than the rate of diffusion of ions to the root surface, and may have been at least as great as the rate of water flux (mass flow) to the roots (Kramer, 1969; Caldwell, 1976). The uptake of nutrients was assumed to be dependent on the amount of soil exploited by the growing roots. It was calculated that 1 cm of root with an average radius of .015 cm could exploit a cylinder of soil 1 cm in length and 1 cm in diameter. That is, for every cm of root material, there would be  $0.7854 \text{ cm}^3$  of soil volume exploited. The processes of mass flow and diffusion and the influence of root hairs, were not modelled, but were assumed to be operative within the root - soil cylinder.





The conversion factor of increase of root length/root mass was 50 m/g dry root weight. Nye and Tinker (1977) used a conversion of 150 m/g but other data cited by them suggested that this factor may be as low as 10 m/g. The conversion factor used in this model is comparatively low, and could be revised in later versions.

### Nitrogen Dynamics

The amount of nitrogen used in the simulation models was varied from a maximum of 60 ppm each of ammonium-N and nitrate-N in the soil, to a minimum of 4 ppm each. It was assumed that all of the ammonium and nitrate were totally in solution. This was acceptable for nitrate; for ammonium, at least one-half or more would be expected to be fixed in soils or participate in exchange reactions. This was not allowed for in the present model but could quite easily be added within the existing framework. It was expected that ammonium would be nitrified and an empirical loss of 20%/day was built into the model. On an hourly basis, this amounted to a reduction of 99.05% of the original ammonium concentration. In this manner, nitrate concentration was increased by the same amount. The concentration of nitrogen was further reduced by the amount of nitrogen taken up by the plant roots. It was assumed that the presence of ammonium would not inhibit the uptake of nitrate, although there is evidence that this process does occur (Lycklama, 1963; Fried *et al*, 1965; Rao and Rains, 1976). Also it was



assumed that there was no water stress on the growing plants and therefore no effects on solution concentration by moisture reduction.

The uptake of nitrogen was assumed to follow Michaelis-Menten kinetics. The  $V_{max}$  of ammonium ( $V_{max1}$ ) or nitrate ( $V_{max2}$ ) was adjusted by multiplying it with the relative uptake rate (RUR, Table 11) with respect to root C/N ratio. The net uptake of N was also assumed to occur only during the day; as such it was switched on 16 hours/day by the variable UT. The uptake of N ( $UNH_4$ ) was calculated in moles of N according to the equation:

$$UNH_4 = (V_{MAX}/(K_{MNH_4} + CNH_4))(CNH_4)(PLANT\ WEIGHT)(UT)$$

The units of  $V_{max}$  were mol N taken up/g plant/h.

### Root Compartments

Two sets of uptake data were calculated for each compartment of root growth, the old root growth and new root growth. The new root growth compartment contains growth resulting from the previous hour, which contacts a new volume of solution concentration of nitrogen ( $CNH_4$ ,  $CNO_3$  in mol/ml) which has not been affected by plant uptake. The old root growth compartment contains the rest of the roots which have grown up to that particular time. The roots in this compartment take up N from the solution nitrogen which remains after previous plant uptake ( $RNH_4$ ,  $RNO_3$  now called residual nitrogen in mol/ml). Old root growth compartment parameters are indicated by the suffix 1, such as  $RC1$ ,  $SOL1$ ,



etc., while new root growth is denoted by the suffix 2 (eg. RC2, VSOL2). A quantity of N ( $Q_{NH_4}$ ,  $Q_{NO_3}$ ) is calculated for each root compartment in mol N. If the uptake of N at any particular time should exceed the quantity of N present, it is set equal to the quantity. This avoids the problems of negative uptake values. The uptake and quantity parameters are used to re-calculate the residual N.

### Shoot Compartment

The total weight (TWT) of the plant is calculated each hour. It is a cumulative parameter and adds the previous total to that hour's new growth, consisting of the product of the shoot carbon (SC), the maximum shoot growth rate (MGR), the relative growth rates with respect to shoot C/N ratio (RGRCN) and age (RGRAGE), and uptake time (UT) in units of 1 hour, and then divided by 45%, the assumed carbon content of the shoot to convert to g weight as follows:

$$TWT = TWT + (SC * MGR * RGRCN * RGRAGE * UT) / 0.45$$

At this time the weight of the new plant growth (WT2) is also calculated:

$$WT2 = TWT - WT1$$

The fraction of carbon translocated downwards (FCT, from McGill *et al*, 1981), is calculated hourly using a CSMP linear function generator and the carbon translocation data (Table 16). The weight of carbon translocated (CT) from the recently assimilated carbon is calculated as follows:

$$CT = WT2 * FCT * 0.45$$



The shoot carbon (SC) is then adjusted by subtracting CT and adding CT on to root carbon (RC).

### Nitrogen Translocation

The amount of root nitrogen (RN, in g) is also a cumulative parameter, and the previous value of RN is added to the current uptake of ammonium and nitrate in moles, from both old (UNH41, UNO31) and new root growth (UNH42, UNO32) and converted to a weight basis as follows:

$$RN = RN + (UNH41 + UNH42 + UNO31 + UNO32) * 14$$

The amount of nitrogen translocated can then be calculated from the ideal relationship (IRAT) between root carbon to nitrogen ratios (RC/RN) and shoot carbon to nitrogen ratios (SC/SN) as follows:

$$\begin{aligned} IRAT &= (RC/RN) / (SC/SN) \\ IRAT &= (RC/RN) * (SN/SC) \\ RN &= (RC/IRAT) * (SN/SC) \end{aligned}$$

after N translocation,

$$\begin{aligned} RN - NT &= ((SN + NT)(RC)) / ((SC * IRAT)) \\ RN - NT &= (SN * RC) / (SC * IRAT) + (NT * RC) / (SC * IRAT) \\ RN - (SN * RC) / (SC * IRAT) &= NT(1 + RC / (SC * IRAT)) \end{aligned}$$

solving for NT,

$$NT = (RN - (SN * RC) / (SC * IRAT)) / (1 + RC / (SC * IRAT))$$

and multiplying both top and bottom by (SC \* IRAT)

$$NT = ((RN * SC * IRAT) - (SN * RC)) / (RC + (SC * IRAT))$$

The parameters RN and SN can then be adjusted for NT as follows:

$$RN = RN - NT$$





$$SN = SN+NT$$

Shoot and root C/N ratios can now be determined as can shoot/root ratios, based on SC and RC.

IRAT was assigned a value of 3.0 up to 15 days, declined linearly to 1.0 by day 100, and was constant thereafter. Further verification of this parameter is necessary.

### Final Controls

Finally a control is placed on the maximum soil solution volume which can be exploited. When the root mass reaches such a size that it is exploiting the maximum volume, the concentration of N is directly reduced by the total amount of uptake. The concentration of N is not allowed to become negative. The residual concentration of nitrate, RNO3, is calculated by:

$$RNO3 = OCN03 + (TQNIT/TVSOL) - (TUNO3/TVSOL)$$

where OCN03 = original concentration of nitrate in solution

TQNIT = total quantity of ammonium nitrified

TVSOL = total volume of soil solution

TUNO3 = total uptake of nitrate

## C. Model Validation

### Introduction

Most of the quantitative information derived from this project was used in the simulation model. There were two measured parameters against which the model could be tested. These were shoot/root ratios and total dry weight.



## Shoot/Root Ratios

A comparison of the simulated and experimental shoot/root ratios (Figures 17 and 18), indicates good agreement for brome. The simulated shoot/root ratios appear to level off about 20 days later than was observed in the experimental data. The agreement is not as good for fescue. The simulated ratios reach a maximum of 4.25 at day 111 compared to experimental data of 5.40 at day 100. The lower simulated shoot/root ratios would tend to overemphasize the roots of fescue.

The simulated data for both species exhibits a "bump" in the first 24 days. This "bump" is related to the carbon translocation data (Table 16). The carbon translocation calculated for brome in the first 26 days was 58%. It was found that a constant value of 0.58 over this time period produced too large a plant, so this value was adjusted downwards to 0.4 in brome. Similarly fescue was adjusted to 0.3 from 0.441 at 21 days. However there is some indication that this "bump" may be real. Root and shoot weight were recorded for some of the fescue seedlings at 15 days and the average shoot/root ratio was 2.61. These seedlings had been deprived of nitrogen for 7 days though and the effect of nitrogen starvation on shoot/root ratio is unknown, although it is likely that shoot growth would proceed at the expense of root growth. Further verification of this parameter is necessary.



## Total Dry Weight

A comparison between simulated dry weights and experimental dry weights for both species indicates simulated growth preceeded the observed experimental growth (Figures 19 and 20). The dry weights for brome are of limited value for validation of the model because they were derived from the means of 15 plants per pot (Table 6). Brome dry weight was very sensitive to overcrowding and so the dry weights used in this validation (Figure 19) were derived from plants grown at a rate of 5 per pot. The experimental growth data for brome are indeed sketchy with a trend curve being interpolated between only 4 data points at 3 time intervals. Brome at 78 days, in ammonium and nitrate uptake experiments, where the plants had been deprived of nitrogen for 10 days, weighed 14.3 and 9.9 g respectively. Brome at 61 days weighed 7.34 g (Table 11) and coincided with the simulated value. There was more growth data for fescue and the simulated values were similar, although not as large a plant was produced (5.5 g vs 5.0 g). The simulation model agreed very well with early plant growth for both species, though, and exhibited the long period of slow growth over the first 50 days in fescue.

## Summary

The model was representative of the two species, brome and fescue. It must be noted that:

1. the simulated total dry weights may be somewhat lower



- than the actual plant weights;
2. the simulated growth attained the exponential phase of growth before the experimental data showed it, especially with fescue and;
  3. the model may tend to overestimate the weight of roots.
- The simulated data also point out the need for better growth data to validate the model and, further, to refine the existing parameters.

#### D. Sensitivity of the Model

##### Introduction

The simulation model was designed to give as much information as possible concerning the growth of two grasses, brome and fescue. One of the basic principles used in the construction of the model was that the roots could only exploit a finite volume of soil and that every cm of root length would exploit a cylinder of soil 1 cm in length with a radius of 0.5 cm. The maximum soil volume that any root mass was allowed to exploit was 16,667 cm<sup>3</sup> which amounted to a cylinder 65 cm in depth and 9 cm in radius. At a constant moisture content of 30%, this would make available to the rooting system, 5,000 ml of soil solution. The maximum amount of nitrogen given to any plant was 60 ppm in soil of ammonium and nitrate (120 ppm N in soil total). These figures were converted to solution concentrations and used in the model. Therefore the parameters against which





the sensitivity of the model can be tested are rooting volume, nitrogen concentration and quantity-intensity relationships of nitrogen and rooting volume.

### Rooting Volume

The volume of soil solution which could be exploited by the roots was varied between 5,000 ml and 1,000 ml for both species, while maintaining the soil levels of nitrogen at 60 ppm each of ammonium and nitrate. For brome there was no significant reduction in either total plant weight or shoot/root ratio when the soil solution volume was reduced from 5,000 to 1,000 ml. However at 2,000 ml volume, brome used up all of the nitrogen available to it by day 115; at 1,000 ml volume, by day 71. Since predicted total weight was not affected, the plant as modelled, must have been using its own reserves of plant nitrogen (Figure 21). The simulation predicted a drop of 0.4% in plant weight between 5,000 ml and 1,000 ml of solution volume (Table 20), with a corresponding reduction of 53.0% in total nitrogen content for brome. At 5,000 ml volume there were 142.9 mmol N available for uptake, of which the brome took 61.1 mmol or 57.2% (Table 20). At 2,000 and 1,000 ml volume, there were 57.1 and 28.6 mmol N available respectively, of which brome utilized 100%. The only experimental data to which this simulation can be compared is the brome starvation experiment (Table 11). There, brome suffered weight losses of 7.9% and 11.4% corresponding to decreases in total N



content of 26% and 42%. The model tends to overemphasize the reduction in plant N content in relation to plant weight with decreasing levels of soil N. This aspect of the model requires further fine tuning.

For fescue, the model predicted no reductions in any plant parameters with a reduction in solution volume from 5,000 to 1,000 ml, providing the soil levels of N were constant at 120 ppm. The total uptake of N by fescue was 12.28 mmol, at 5,000 ml, of 142.9 mmol N available, or 8.6%. At 1,000 ml solution volume, there were 12.34 mmol N taken up from 29.84 mmol N available in the system, an uptake of 41.4%. However, where these figures are converted to uptake/g plant, under conditions of unlimited soil volume and soil nitrogen (5,000 ml and 120 ppm N), brome had an uptake of 3.13 mmol/g plant compared to 2.46 mmol/g plant for fescue. On a relative scale, fescue was 27% more efficient at converting nitrogen to dry weight.

The simulated total N content in fescue over 120 days (Figure 22) showed no reduction in N content with decreasing solution volume. The simulation of plant N content does not agree well with the experimental data, and tends to underestimate plant N over the first 75 days.

### Soil Nitrogen Concentration

In decreasing soil nitrogen levels, the solution volume was held constant at 5,000 ml and soil nitrogen was reduced from 120 ppm to 8 ppm N for Magna brome. There is a marked



decrease in total N content of the plant (Figure 23). The model indicates that the plant can lose up to almost 50% of its stored reserves of nitrogen while experiencing only a 16% reduction in plant weight (Table 18). Further utilization of plant N results in a very much reduced plant weight. The simulated data compare favourably with the experimental data (Table 11) for nitrogen starvation, where a 15 day period of N starvation resulted in a decrease in plant weight of 11.4% and a decrease in N content of 42%.

There are other plant parameters which change with decreased soil nitrogen. The C/N ratios in the roots and shoots increase dramatically. At soil levels of 8 ppm the shoot C/N ratio exceeds 50 by day 96, thus stopping further growth, although the total uptake of nitrogen remained high (Table 18). As the soil nitrogen was reduced the efficiency of conversion of absorbed N to dry weight increased sharply. The weight loss associated with a 50% reduction in plant N content may be variable, but, this value could be used as an index to compare the relative uptake of N between brome and fescue. For brome, the 50% reduction in plant N content from a soil with unlimited rooting volume and varying levels of soil N would correspond to an uptake of 1.5 mmol N/g plant. At N uptake rates less than 1.5 mmol N/g plant, it could be expected that the reduction in plant weight would be quite significant.

The response of fescue to varying nitrogen levels at 5,000 ml of solution volume appeared to be rather similar to





brome (Figure 24 and Table 19). Fescue was more efficient than brome at converting absorbed N to plant dry matter only at 120 ppm soil N. The efficiency was more or less equivalent at the lower levels of soil N. This would indicate that fescue tends to accumulate less nitrogen than brome at higher levels of soil N and a corollary of this would be that fescue has less stored reserves of nitrogen.

The simulation model predicted that at high levels of soil N, fescue, the slow-growing native species, is more efficient in its uptake of nitrogen per unit weight of plant than the fast-growing agronomic species, brome. During periods of nitrogen stress, both fescue and brome experienced similar weight reductions. When nitrogen became very limiting, the shoot/root ratios were reduced for both species.

### Nitrogen Quantity-Intensity Relationships

In this series of tests, the solution volume was reduced to 1,000 ml and the soil N content was varied between 120 and 10 ppm for both species. For fescue, there was no difference whether the simulation was conducted at 5,000 or 1,000 ml of solution volume (Table 19). The roots of fescue could fully exploit 1,000 ml of solution only by 106 days and at this point the rate of growth had been slowed down in the model.

For brome, the plant N followed a similar pattern as in previous simulation runs except that there was a sharp break





when the external concentration of soil N was exhausted and the plant was forced to redistribute its own reserves of nitrogen (Table 20). As the soil levels were reduced, the plant exhausted the external soil N earlier in its growth cycle (Figure 25).

At a limiting solution volume, the soil N level which produced a 50% reduction in plant N content yielded no reduction in plant weight, whereas the data in Table 18 suggested that a 50% reduction in plant N would produce a 20% reduction in plant weight. This relationship between reduction in plant weight and plant N content is shown in Figure 26. When the rooting volume becomes limiting or the amount of N present is limiting, the model predicts a negative feedback relationship (Table 21).

The amount of N taken up by brome increases between 120 and 30 ppm soil N at 5,000 ml solution volume. But between 30 and 8 ppm, the uptake decreases. This would suggest that at these low levels of soil N, there is insufficient N to allow brome to grow enough roots to fully exploit the available N. At 1,000 ml solution volume, brome fully exploits soil N. Similarly, the model predicts that fescue uptake of N increases between 120 and 30 ppm soil N, and decreases between 30 and 10 ppm, at solution volumes of either 5,000 or 1,000 ml. This possible feedback relationship warrants further investigation.

The model predicted that both fescue and brome are subject to nitrogen stress but for different reasons. Brome



consistently takes up more nitrogen, at every level of available nitrogen, than does fescue. Therefore it is predicted that brome suffers nitrogen stress because it depletes the system of N and is forced to redistribute its own reserves of stored N. Fescue takes up much less N at every level of soil N than brome, except at 1,000 ml solution volume and 30 ppm soil N, where brome takes up 100% of the available nitrogen by day 54; fescue by day 117. In examining the output of the simulation model, it was predicted that the reason that fescue is limited in its ability to extract N, is because its roots do not grow fast enough, thus resulting in very high root and shoot C/N ratios. In the simulation model, as the shoot C/N ratio increases, the relative growth rate decreases, until at shoot C/N ratio of 50, growth is halted.

## Summary

The simulation model does not represent plant N content accurately and gives a somewhat distorted and simplistic view of the internal cycling of N. Experimental data suggested that there may be a 4:1 reduction in plant N content:dry weight for brome (Table 11, discussion p. 58). Such a relationship is also implied by the model (Figure 26). A negative feedback relationship is also indicated by the model, especially for fescue, suggesting that roots increase in size with decreasing levels of soil N down to a certain critical initial value, after which the roots also



decrease in size. The uptake of N parallels the pattern of root development and growth. The simulation also predicts that as the levels of soil N are decreased in sequential runs, the shoot:root ratios are also slightly reduced.

## E. Implications for Reclamation

### Introduction

The two grasses considered in the model are very different. brome is a fast-growing, tillering agronomic species; fescue is a slower-growing native bunchgrass. The experimental data for the uptake of ammonium or nitrate did not reveal any fundamental differences between the two grasses, however. Over the low concentration range (0.005-0.1 mM), the  $K_m$  values (an index of the ability of the plant to take up nitrogen) of brome and fescue were similar for ammonium uptake, and over the high concentration range (0.1-5.0 mM) brome had a distinct advantage in uptake only at the seedling stage, as indicated by a lower  $K_m$  than fescue. There were no significant differences in the ability of brome or fescue to absorb nitrate, neither over both concentration ranges nor at 15 or 79 days of age. Both brome and fescue were able to extract nitrogen, whether in ammonium or nitrate form, from similar low solution concentrations. Brome tended to have a slightly higher maximum uptake rate for ammonium at 15 days, but at 78 days, fescue had a higher  $V_{max}$  value. On the basis of the kinetic



data presented, there would appear to be no differences in the behaviour of these two grasses with regard to nitrogen uptake.

The growth data indicated that brome was a much larger plant and it was surmized that the differences in plant size were genetically controlled and directed by the internal cycling of carbon and nitrogen, rather than the uptake of nitrogen, directly.

The simulation model mathematically computed growth every hour, 16 hours/day for 120 days. It was basically driven by the shoot and root C/N ratios and interactions of the two parameters. The constants used in the model were derived from experimental data under ideal conditions. The grasses were subject only to nitrogen stress.

### Implications for Reclamation

It was predicted in the previous chapter from output of the simulation model, that fescue was much more efficient at absorbing N than brome when rooting volume and soil nitrogen levels were not limiting. However when nitrogen levels and rooting volume were reduced, both grasses were subject to nitrogen stress. The model predicted that brome would be subject to nitrogen stress because it had exhausted soil N levels and that fescue would be unable to grow enough roots to take up sufficient nitrogen to meet the demands of shoot growth.





The simulation appears to explain the observations of Berg (1974) and others that brome dominates a stand when fertilized heavily, and that fescue generally grows better in open, disturbed sites than in undisturbed areas when competing with other grasses. Fescue, with its slow growth rate and shallow rooting system would not fare too well if mixed in with brome. There may also be other effects on fescue, such as tolerance to shading.

The model assumed no moisture stress on the plants, and did not examine any losses from the plants either. Grasses do lose nitrogen in the form of exudates from the roots (Nye and Tinker, 1977). Also, significant amounts of N may be volatilized from the leaves, and this may be greatest in plants well supplied with nitrogen and actively transpiring (Lemon and Van Houtte, 1980). Brome was observed to show signs of nitrogen deficiency during the starvation prior to an uptake experiment, while there was no such effect observed on fescue. Brome was also observed to be susceptible to moisture stress at later stages of growth and especially when raised at 15 plants per pot. Wilting was never observed in fescue, at any density. It is surmized that fescue may be more efficient than brome in its internal use of both nitrogen and water. This is not indicated in the simulation and indicates that further refinement is needed in the fescue model.

The model only operates over the first growing season. Chapin (1980) indicated that slower growing species tended



to live longer than fast-growing species. If this longevity of growth applied to the rooting system, then in following years fescue could develop a larger root mass than brome which could certainly give it a competitive advantage over brome, in increased resistance to moisture and nitrogen stress. At such time as the root system was more fully developed, the relative efficiency of fescue in converting absorbed N to plant dry matter should become more apparent. On the other hand, if brome roots were to be almost completely renewed every season, it would not increase its competitive advantage, especially once maintenance fertilization was stopped in a reclamation situation.

The other two grasses used in this study, needlegrass and wheatgrass were not modelled. However based on their growth data and their nitrogen uptake characteristics, wheatgrass would be expected to behave in a manner very similar to brome, while needlegrass would be expected to be somewhere in between fescue and brome.

The model demonstrated the need for more information about the internal cycling of carbon and nitrogen in the plant and how this cycling changes according to phenology. There is highly sophisticated research currently ongoing at Duke University by Goetschl where a grass plant is being grown in a laboratory adjacent to a cyclotron, which can generate a continuous supply of  $^{11}\text{C}$  and  $^{13}\text{N}$ .  $^{11}\text{C}$  has a half life of about 20 minutes;  $^{13}\text{N}$  about 10 minutes. Therefore there is no buildup of background levels. The plant can be



set up over one detector for the shoots and another for the roots and the dynamic interchange of carbon and nitrogen in a grass can be monitored over the entire life span of the plant. When this research is published it will certainly be a definitive work in the field of carbon translocation in grasses.

In the model an arbitrary relationship between root C/N ratio and shoot C/N ratio was applied to both brome and fescue. This resulted in plant nitrogen contents which were lower than those observed experimentally over the first 60 days. While this difference likely would have had little effect on the simulated growth, it would be desirable to refine this aspect of the model to more closely approximate actual conditions.

Another subject which needs more attention is the root system, especially in the context of reclamation. It is the below-ground portion of the plant which is responsible for stabilizing soil, yet few studies attempt to quantify or even estimate the root mass. Information is also needed on rates of root extension in native grasses, as well as the spatial distribution and seasonal turnover of roots.

It is doubtful that a similar study need be attempted to corroborate the present findings of nitrogen uptake by native grasses. There does not appear to be a great deal of difference between the kinetic functioning of various grasses, agronomic or native. If further studies on native grasses were undertaken, a simple pot study could yield much



more relevant data if root and shoot dry weights, carbon and nitrogen measurements, root length and leaf area index were recorded according to the phenology of the plant. The maximum uptake rate,  $V_{max}$ , can be inferred from such information, and a literature value of  $K_m$  could be used quite successfully.

This simulation model could be used as a screening tool to evaluate other native grasses and their nitrogen uptake characteristics, once the refinements and adjustments already discussed are inserted into the model. It could be used to utilize and summarize the data collected in a single pot experiment conducted at optimum soil levels of nitrogen. The behaviour of the plant to various stresses could then be evaluated. In the present format, it would not be difficult to include statements for moisture and temperature effects on plant growth. The model does not provide an exact re-creation of plant growth but does indicate some very significant trends in the growth of native grasses.





## XII. Conclusions

From this study, several conclusions can be drawn regarding the growth and nitrogen uptake characteristics of fescue, needlegrass, wheatgrass and brome.

1. The  $K_m$  values, for ammonium and nitrate, are similar for all grasses, native and agronomic, over both low and high concentration ranges.
2. There are dual patterns of uptake for both ammonium and nitrate for all grasses, native or agronomic.
3. There is an indication that slower growing grasses may be more efficient in their use of nitrogen than faster growing grasses and this may be more apparent in succeeding years.
4. All grasses, native or agronomic, can extract nitrogen with equal ability from the same low solution concentrations.
5. The simulation model integrates and organizes all of the experimental data. It indicates significant long term trends in the uptake behaviour of grasses, as well as indicating areas where future research should be directed.
6. The simulation model should be expanded to include moisture and temperature effects, and could be used as an analytical tool to assess the nitrogen uptake characteristics of other grasses and their response to stresses.



**TABLES**

**FIGURES**

**BIBLIOGRAPHY**

**APPENDICES**



### XIII. Tables



Table 1. Michaelis Constants of Uptake Experiments for Low Concentration Ranges

Ion	K <sub>m</sub> (mM)	Plant Species	Reference
NH <sub>4</sub>	0.1	Maize	van den Honert and Hooymans (1961)
NH <sub>4</sub>	0.04	Perennial rye	Lycklama (1963)
NH <sub>4</sub>	0.02	Rice roots	Fried <i>et al</i> (1965)
NH <sub>4</sub>	0.021	Corn	Edwards and Barber(1976)
NO <sub>3</sub>	0.021	Maize	van den Honert and Hooymans (1955)
NO <sub>3</sub>	0.6	Rice roots	Fried <i>et al</i> (1965)
NO <sub>3</sub>	0.033	Perennial rye	Lycklama (1963)
NO <sub>3</sub>	0.021	Corn	Edwards and Barber(1976)
NO <sub>3</sub>	0.11	Barley	Rao and Rains (1976)

Table 2. Physical Properties of Growth Medium

Particle Size Analysis Range	0.1 - 0.5 mm
Bulk Density	1.60 g/cm <sup>3</sup>
Porosity	40%
Hydraulic Conductivity	68.4 cm/h

Table 3. Macronutrients in Nutrient Solution (ppm)

Ions/ Elements/ Ratios	Shive and Robbins (1942)	Johnson <i>et al</i> (1957)	Paton
NO <sub>3</sub> -N	111.0	196.0	112.0
NH <sub>4</sub> -N	19.0	28.0	28.0
Ca	159.0	160.0	160.0
K	89.0	234.0	127.0
S	96.0	32.0	96.0
P	71.0	62.0	73.0
Mg	56.0	24.0	44.0
pH	5.5	6.0	5.9
NO <sub>3</sub> /NH <sub>4</sub>	5.8	7.0	4.0
Ca/Mg	2.8	6.7	3.6





Table 4. Micronutrients in Nutrient Solution  
(after Epstein, 1972)

Chemical	Stock Solution		Final Solution
KCl	3.728 g/l	50.0 mM	
H <sub>3</sub> BO <sub>3</sub>	1.546	25.0	
MnSO <sub>4</sub> ·H <sub>2</sub> O	0.338	2.0	
ZnSO <sub>4</sub> ·7H <sub>2</sub> O	0.575	2.0	1.0 ml/l
CuSO <sub>4</sub> ·5H <sub>2</sub> O	0.125	0.5	
H <sub>2</sub> MoO <sub>4</sub>	0.081	0.5	
NaCl	0.029	0.5	
FeEDTA	6.922	20.0	1.0 ml/l

Table 5. Comparison of Macronutrients in Nutrient Solutions  
With and Without Nitrogen (ppm)

Element /Ion	+Nitrogen <sup>1</sup>	-Nitrogen <sup>2</sup>
Ca	160	80-280 <sup>3</sup>
Mg	44	44
K	127	127
PO <sub>4</sub> -P	73	73
SO <sub>4</sub> -S	96	128-280 <sup>4</sup>

<sup>1</sup>fixed amounts of Ca(NO<sub>3</sub>)<sub>2</sub> and (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>

<sup>2</sup>N-free solution, also used as base for uptake solutions with labelled N added

<sup>3</sup>depending on amount of Ca(<sup>15</sup>NO<sub>3</sub>)<sub>2</sub> used

<sup>4</sup>depending on amount of (<sup>15</sup>NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> used



Table 6. Dry Weights of Plants Grown at 15 Plants per Pot

Species	Growth (Days)	Shoot Wt. (g)	Root Wt. (g)	Plant Wt. (g)	Shoot/ Root
Fescue	0			0.00079 <sup>1</sup>	
	41	0.15	0.11	0.26	1.27
	72	0.90	0.29	1.19	3.17
	90	1.44	0.30	1.74	4.85
	100	2.11	0.39	2.50	5.40
	116	3.70	0.82	4.52	4.51
	131	4.48	1.04	5.52	4.31
Needlegrass	0			0.002 <sup>1</sup>	
	34	0.14	0.07	0.21	2.00
	47	0.42	0.20	0.62	2.09
	61	1.03	0.42	1.45	2.43
	69	1.51	0.47	1.98	3.21
	80	3.35	0.78	4.13	4.32
	93	3.81	2.46	6.27	1.55
	107	6.13	2.13	8.26	2.88
	120	6.03	2.30	8.33	2.62
Wheatgrass	0			0.003 <sup>1</sup>	
	33	0.34	0.25	0.59	1.36
	50	1.49	0.80	2.29	1.87
	57	1.80	0.92	2.72	1.96
	70	2.91	1.12	4.03	2.60
	83	3.51	1.56	5.07	2.65
Brome	0			0.0035 <sup>1</sup>	
	26	0.13	0.17	0.30	0.73
	34	0.29	0.25	0.54	1.18
	74	3.43	0.95	4.38	3.61
	82	4.65	1.17	5.82	3.97

<sup>1</sup>seed weight



Table 7. Effect of Plant Age on Total N Content

Species	Age	%N	Species	Age	%N
Fescue	29	4.06	Needle-grass	33	5.05
	31	3.55		44	2.47
	36	3.52		50	3.32
	53	3.92		55	2.71
	54	3.73		73	3.14
	64	3.23		84	2.56
	115	2.60		85	2.08
Wheatgrass	28	3.81	Brome	25	4.53
	33	3.94		31	4.59
	39	3.22		36	3.55
	43	3.46		43	2.26
	55	2.60		45	3.14
	61	3.01		61	3.25
	66	2.92			
	77	2.47			

Table 8. Effect of Planting Density on Total Plant Weight

Species	Age	15/Pot Wt.	5/Pot Wt.	Species	Age	15/Pot Wt.	5/Pot Wt.
Fescue	41	0.26		Needle-grass	34	0.21	
	72	1.19			44		0.73
	78		1.59 <sup>1</sup>		47	0.62	
	90	1.74			61	1.45	
	100	2.50			69	1.98	
	116	4.52			78		4.02 <sup>1</sup>
	131	5.52			80	4.13	
Wheat-grass				Brome	93	6.27	
	33	0.59			26	0.30	
	50	2.29			31		0.76
	57	2.72			34	0.54	
	58		3.41 <sup>1</sup>		36		1.59
	70	4.03			43		2.39
	78		7.48 <sup>1</sup>		55	2.54	
	83	5.07			61		7.34
					74	4.38	
					78		12.08 <sup>1</sup>
					82	5.82	

<sup>1</sup>data taken from uptake experiments where plants had been starved of N between 10 and 14 days



Table 9. Ammonium Uptake Results For Fescue, Needlegrass, Wheatgrass and Brome Grown at 15 Plants/Pot and Without Aeration in the Uptake Solutions

Species /Age	Parameter	Concentration Range		Corrected High <sup>1</sup>
		Low	High	
Fescue 50 Days	Vmax <sup>2</sup>	0.078±.042 <sup>4</sup>	0.321±.085	0.243±.085
	Km <sup>3</sup>	0.025±.025	0.596±.430	0.571±.430
	r <sup>2</sup>	0.59(2-8)	0.87(10-14)	
Fescue 99 Days	Vmax	0.033±.009	0.171±.069	0.138±.069
	Km	0.035±.018	1.21±.85	1.18±.85
	r <sup>2</sup>	0.84(3-9)	0.80(9-14)	
Needle- grass 41 Days	Vmax	0.085±.038	0.283±.066	0.198±.066
	Km	0.021±.016	0.284±.210	0.263±.210
	r <sup>2</sup>	0.76(2-7)	0.86(9-14, -11)	
Needle- grass 87 Days	Vmax	0.030±.015	0.091±.021	0.016±.021
	Km	0.037±.032	0.310±.223	0.273±.223
	r <sup>2</sup>	0.72(3-9)	0.79(9-14)	
Wheat- grass 58 Days	Vmax	0.083±.022	0.221±.089	0.138±.089
	Km	0.020±.010	0.226 <sup>5</sup>	0.242 <sup>5</sup>
	r <sup>2</sup>	0.84(2-8)	0.64(11-14)	
Brome 87 Days	Vmax	0.026±.009	0.089±.035	0.063±.035
	Km	0.027±.017	0.461±.460	0.434±.460
	r <sup>2</sup>	0.90(3-8, -6)	0.90(9, 11, 13, 14)	

<sup>1</sup>Corrected High = low range values subtracted from high range values

<sup>2</sup>Vmax = mg N taken up/g plant/2 hr

<sup>3</sup>Km = mM

<sup>4</sup>95% confidence interval for most data

<sup>5</sup>Less than 90% confidence that number is significantly different from zero





Table 10. The Uptake of Ammonium by Fescue From Solutions With and Without Other Nutrient Ions at 78 Days

Treat- ment	Para- meter	Concentration Range		
		Low	High	Corrected High <sup>1</sup>
With Nutrient Ions	Vmax <sup>2</sup>	0.126±.024 <sup>4</sup>	0.464±.102	0.338±.102
	Km <sup>3</sup>	0.013±.005	0.334±.172	0.321±.172
	r <sup>2</sup>	0.91(2-8,-5)	0.83(8-14)	
Without Nutrient Ions	Vmax	0.147±.035	0.355±.022	0.208±.035
	Km	0.016±.008	0.345±.064	0.329±.064
	r <sup>2</sup>	0.79(1-9)	0.98(9-14)	

<sup>1</sup>Corrected High = low range values subtracted from high range values

<sup>2</sup>Vmax = mg N taken up/g plant/2 hr

<sup>3</sup>Km = mM

<sup>4</sup>95% confidence interval for most data



Table 11. Effect of N Starvation on Uptake of Ammonium by Brome at 61 Days

Parameter	Starvation Period (Days)			
	0	5	10	15
Plant Wt	7.34±3.12 <sup>4</sup>	7.42±1.53	6.76±3.36	6.50±1.11
Total %N	3.25±.39	2.86±.31	2.41±.33	1.90±.18
%Exc. <sup>15</sup> N	0.031±.012	0.063±.042	0.112±.030	0.118±.042
C/N Ratio <sup>1</sup>	13.85	15.73	18.67	23.68
RUR <sup>2</sup>	0.23	0.47	0.91	1.00
RURNGPN <sup>3</sup>	0.14	0.31	0.72	1.00

<sup>1</sup>weight C/weight N; assuming 45% C in plant

<sup>2</sup>Relative Uptake Rate of N/g plant =

(% excess <sup>15</sup>N/plant weight; relative to highest ratio at 15 days)

<sup>3</sup>Relative Uptake Rate of N/g plant N =

(%excess <sup>15</sup>N/((total %N)(plant wt.)));

relative to highest ratio at 15 days)

<sup>4</sup>limits are ± standard deviation



Table 12. Ammonium Uptake Results For Fescue, Needlegrass, Wheatgrass and Brome at Two Ages

Species /Age	Parameter	Concentration Range		
		Low	High	Corrected High <sup>1</sup>
Fescue 15 Days	Vmax <sup>2</sup>	0.226±.035 <sup>4</sup>	0.625±.120	0.399±.120
	Km <sup>3</sup>	0.019±.006	0.870±.375	0.851±.375
	r <sup>2</sup>	0.90(2-9)	0.95(10-14)	
Fescue 78 Days	Vmax	0.126±.024	0.464±.102	0.338±.078
	Km	0.013±.005	0.334±.172	0.321±.172
	r <sup>2</sup>	0.91(2-8, -5)	0.83(8-14)	
Needle- grass 15 Days	Vmax	0.141±.033	0.641±.138	0.500±.138
	Km	0.014±.006	1.330±.540	1.320±.54
	r <sup>2</sup>	0.90(2-8)	0.95(10-14)	
Needle- grass 78 Days	Vmax	0.074±.020	0.200±.102	0.126±.102
	Km	0.039±.023	1.060±1.03	1.02±1.03
	r <sup>2</sup>	0.79(4-10)	0.91(10-14, -13)	
Wheat- grass 15 Days	Vmax	0.458±.081	0.814±.112	0.356±.112
	Km	0.014±.005	0.176±.107	0.162±.107
	r <sup>2</sup>	0.90(2-8)	0.84(9-14)	
Wheat- grass 78 Days	Vmax	0.025±.004	0.058±.016	0.033±.016
	Km	0.014±.005	0.346±.275	0.332±.275
	r <sup>2</sup>	0.89(2-9)	0.75(9-14)	
Brome 15 Days	Vmax	0.445±.031	0.875±.201	0.430±.201
	Km	0.023±.002	0.240±.189	0.217±.189
	r <sup>2</sup>	0.99(1-8)	0.84(9-14, -12)	
Brome 78 Days	Vmax	0.054±.020	0.188±.026	0.134±.026
	Km	0.014±.012	0.416±.153	0.402±.153
	r <sup>2</sup>	0.58(2-9)	0.95(9-14)	

<sup>1</sup>Corrected High = low range values subtracted from high range values

<sup>2</sup>Vmax = mg N taken up/g plant/2 hr

<sup>3</sup>Km = mM

<sup>4</sup>95% confidence interval for all data



Table 13. Nitrate Uptake Results For Fescue, Needlegrass, Wheatgrass and Brome at Two Ages

Species /Age	Parameter	Concentration Range		Corrected High <sup>1</sup>
		Low	High	
Fescue 16 Days	Vmax <sup>2</sup>	0.209±.037 <sup>4</sup>	0.391±.067	0.182±.067
	Km <sup>3</sup>	0.014±.013	0.898±.536	0.884±.536
	r <sup>2</sup>	0.69(4-10)	0.96(11-14)	
Fescue 79 Days	Vmax	0.069±.015	0.119±.061	0.050±.061
	Km	0.016 <sup>6</sup>	0.556 <sup>6</sup>	0.540 <sup>6</sup>
	r <sup>2</sup>	0.58(5-10,-7)	0.76(10-13)	
Needle- grass 15 Days	Vmax	0.240±.029	0.616±.383	0.376±.383
	Km	0.024±.002	1.340±1.21 <sup>5</sup>	1.32±1.21 <sup>5</sup>
	r <sup>2</sup>	0.83(6-10)	0.84(10-14,-13)	
Needle- grass 84 Days	Vmax	0.073±.006	0.230±.116	0.157±.116
	Km	0.091±.001	1.85±1.41 <sup>5</sup>	1.76±1.41 <sup>5</sup>
	r <sup>2</sup>	0.99(6-10)	0.76(10-14)	
Wheat- grass 17 Days	Vmax	0.216±.023	0.721±.169	0.505±.169
	Km	0.017±.008	1.37±.65	1.35±.65
	r <sup>2</sup>	0.89(4-10)	0.90(9-14)	
Wheat- grass 79 Days	Vmax	0.025±.006	0.148±.115	0.123±.115
	Km	0.111±.061	4.39±3.95 <sup>5</sup>	4.28±3.95 <sup>5</sup>
	r <sup>2</sup>	0.86(5-10)	0.70(10-14)	
Brome 15 Days	Vmax	0.241±.059	0.549±.326	0.308±.326
	Km	0.012±.009	1.04 <sup>6</sup>	1.03 <sup>6</sup>
	r <sup>2</sup>	0.65(2-9)	0.72(11-14)	
Brome 80 Days	Vmax	0.025±.007	0.073±.041	0.048±.041
	Km	0.039±.026	0.799±.783 <sup>5</sup>	0.760±.783 <sup>5</sup>
	r <sup>2</sup>	0.88(4-8)	0.66(9-13)	

<sup>1</sup>Corrected High = low range values subtracted from high range values

<sup>2</sup>Vmax = mg N taken up/g plant/2 hr

<sup>3</sup>Km = mM

<sup>4</sup>95% confidence interval for most data

<sup>5</sup>90% confidence interval

<sup>6</sup>Less than 90% confidence that number is significantly different from zero





Table 14. The Uptake of Ammonium and Nitrate by Roots and Shoots of Brome at 78 Days

Part /Ion	Para- meter	Concentration Range		Corrected High <sup>1</sup>
		Low	High	
Roots NH <sub>4</sub>	Vmax <sup>2</sup>	0.093±.035 <sup>4</sup>	0.375±.093	0.282±.093
	Km <sup>3</sup>	0.015±.012	0.655±.358	0.640±.358
	r <sup>2</sup>	0.58(2-9)	0.87(9-14)	
Shoots NH <sub>4</sub>	Vmax	0.008±.001	0.042±.024	0.034±.024
	Km	0.002±.002 <sup>5</sup>	0.857±.828 <sup>5</sup>	0.855±.828 <sup>5</sup>
	r <sup>2</sup>	0.54(2-8)	0.66(10-14)	
Roots NO <sub>3</sub>	Vmax	0.024±.009	0.065±.013	0.041±.013
	Km	0.015 <sup>6</sup>	0.248±.240	0.233±.240
	r <sup>2</sup>	0.52(4-8)	0.78(9-13)	
Shoots NO <sub>3</sub>	Vmax	0.007±.001	0.073±.041	0.066±.041
	Km	0.002±.002 <sup>5</sup>	0.799±.783 <sup>5</sup>	0.797±.783 <sup>5</sup>
	r <sup>2</sup>	0.52(1-7)	0.66(9-13)	

<sup>1</sup>Corrected High = low range values subtracted from high range values

<sup>2</sup>Vmax = mg N taken up/g plant/2 hr

<sup>3</sup>Km = mM

<sup>4</sup>95% confidence interval for most data

<sup>5</sup>90% confidence interval

<sup>6</sup>Less than 90% confidence that number is significantly different from zero



Table 15. Ammonium and Nitrate Uptake and Translocation in  
Brome at 78 Days

Conc.	Mg N Up/g Plant/2 h		% Uptake Translocated	
(mM)	NH <sub>4</sub>	NO <sub>3</sub>	NH <sub>4</sub>	NO <sub>3</sub>
0.0025	0.016		47.6	
0.005	0.016	0.009	30.4	53.5
0.0075	0.016	0.011	37.4	56.5
0.01	0.016	0.013	34.4	50.5
0.025	0.024	0.010	28.3	52.7
0.05	0.038	0.014	21.1	46.9
0.075	0.046	0.016	17.6	41.9
0.1	0.055	0.016	16.3	45.9
0.25	0.071	0.023	26.1	45.7
0.5	0.099	0.029	17.5	53.3
0.75	0.122	0.027	14.2	61.7
1.0	0.139	0.045	14.6	35.5
2.5	0.147	0.055	19.5	63.0
5.0	0.183	0.069	23.4	67.5
10.0		0.146		79.3



Table 16. Carbon Translocation and Plant Age in Brome and Fescue

Brome			Fescue		
Days	%C	Translocated	Days	%C	Translocated
0	40.0		0	30.0	
26	58.0		21	44.1	
30	33.0		56	20.6	
54	18.0		94	16.1	
79	15.3		110	16.1	
110	15.3		120	100.0	
120	100.0				

Table 17. Data For Change in Relative Growth Rate (RGR) With Respect to Age

Brome		Fescue	
Days	RGR	Days	RGR
0	1.00	0	1.00
15	1.00	15	1.00
26	0.589	56	0.25
46	0.18	120	0.0
71	0.0697		
120	0.0		

Table 18. Predicted Effect of Reduced Levels of Soil N on Weight and N Content of Brome by Simulation Model  
(120 Days and 5,000 ml Solution Volume)

Soil N (ppm)	Plant Wt.(g)	Total %N	% Reduction		mmol N up /g plant
			Wt.	%N	
120	19.5	4.38	---	---	3.13
30	16.3	2.35	16.4	46.3	1.68
15	10.3	1.25	47.2	71.5	0.89
8	3.1	0.88	84.1	79.9	0.62



Table 19. Predicted Effect of Reduced Levels of Soil N on Weight and N Content of Fescue by Simulation Model

(120 Days and 5,000 ml or 1,000 ml Solution Volume)

Soil N (ppm)	Plant Wt.(g)	Total %N	% Reduction Wt.      %N		mmol N up /g plant
120	4.98	3.45	---	---	2.47
30	4.39	2.37	11.8	31.3	1.69
15	2.34	1.23	53.0	64.3	0.88
10	0.86	0.94	82.7	72.8	0.67

Table 20. Predicted Effect of Reduced Levels of Soil N on Weight and N Content of Brome by Simulation Model

(120 Days and 1,000 ml Solution Volume)

Soil N (ppm)	Plant Wt.(g)	Total %N	% Reduction Wt.      %N		mmol N up /g plant
120	19.5	2.06	0.4	53.0	1.47
60	15.8	1.27	19.1	71.0	0.90
30	10.2	0.98	47.6	77.6	0.70
15	5.7	0.88	70.7	79.9	0.63
10	4.0	0.85	79.6	80.6	0.60

Table 21. Predicted Percent of Available N Taken Out of Solution by Brome and Fescue by Simulation Model

Solution Volume	Soil N (ppm)	mmol N Avail.	% of Avail. N Taken Up Brome      Fescue	
5000	120	142.9	42.8	8.6
5000	30	35.7	76.6	20.8
5000	15	17.9	51.4	11.5
5000	10	11.9		4.9
5000	8	9.5	20.5	
1000	120	28.6	100.0	43.1
1000	30	7.1	100.0	100.0
1000	15	3.6	100.0	91.7
1000	10	2.4	100.0	24.1





FIGURES

BIBLIOGRAPHY

APPENDICES



#### XIV. Figures



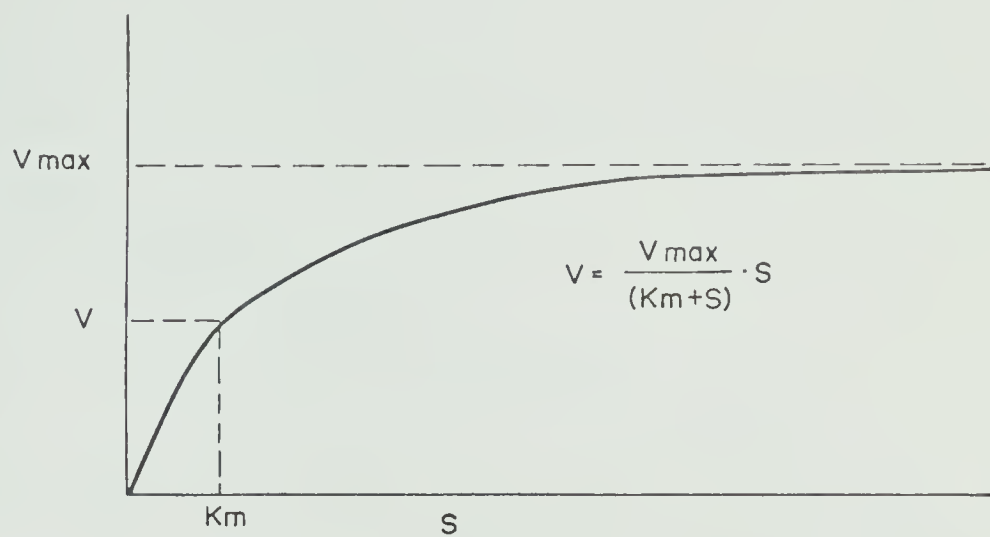


FIGURE 1. TYPICAL PLOT OF MICHAELIS-MENTEN KINETICS

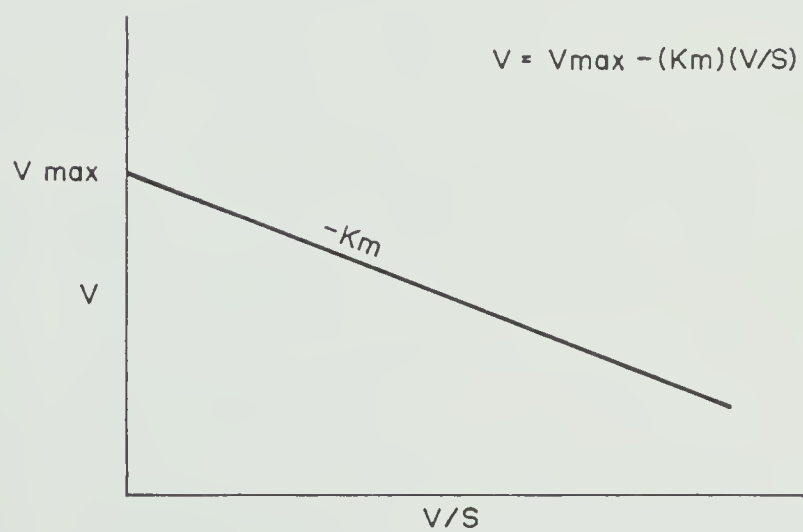


FIGURE 2. THE HOFSTEE TRANSFORMATION OF THE MICHAELIS-MENTEN PLOT



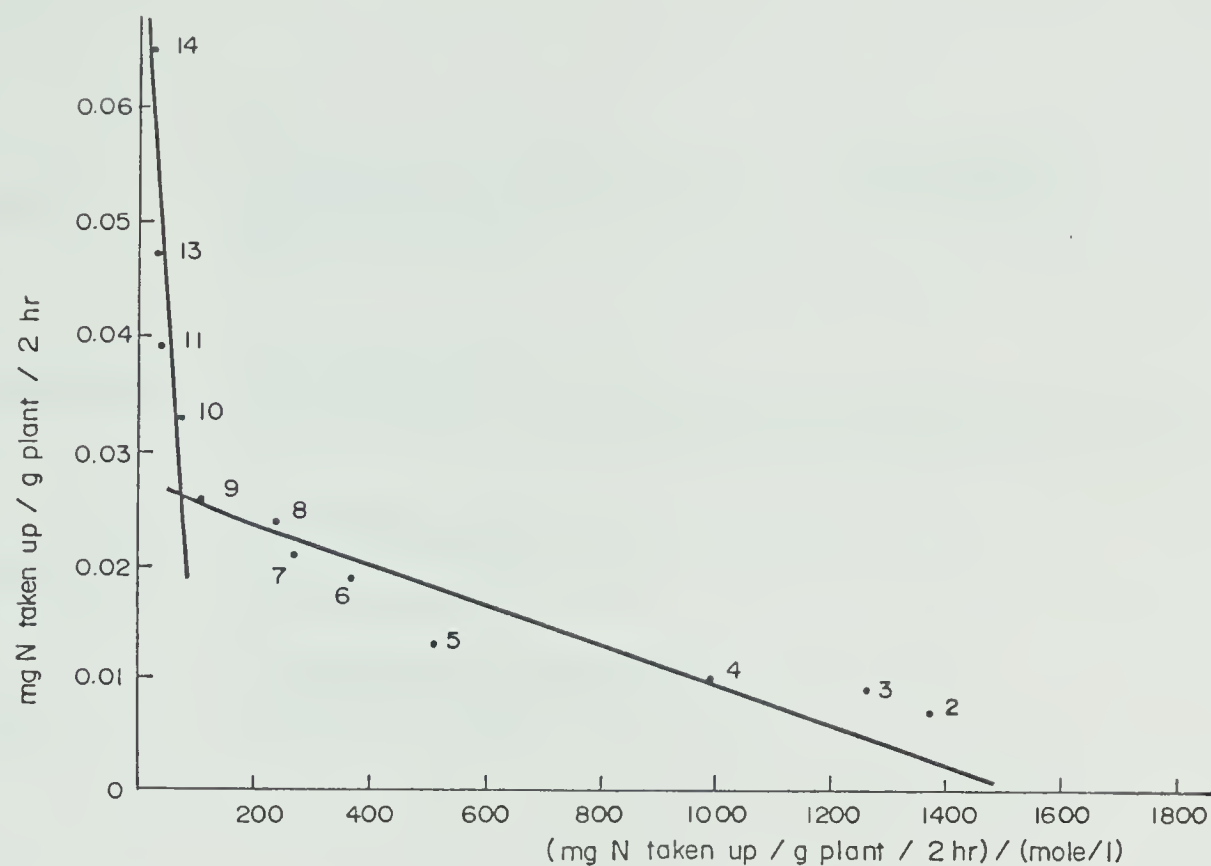


FIGURE 3. HOFSTEE PLOT OF AMMONIUM UPTAKE FOR WHEATGRASS AT 78 DAYS USING MEANS

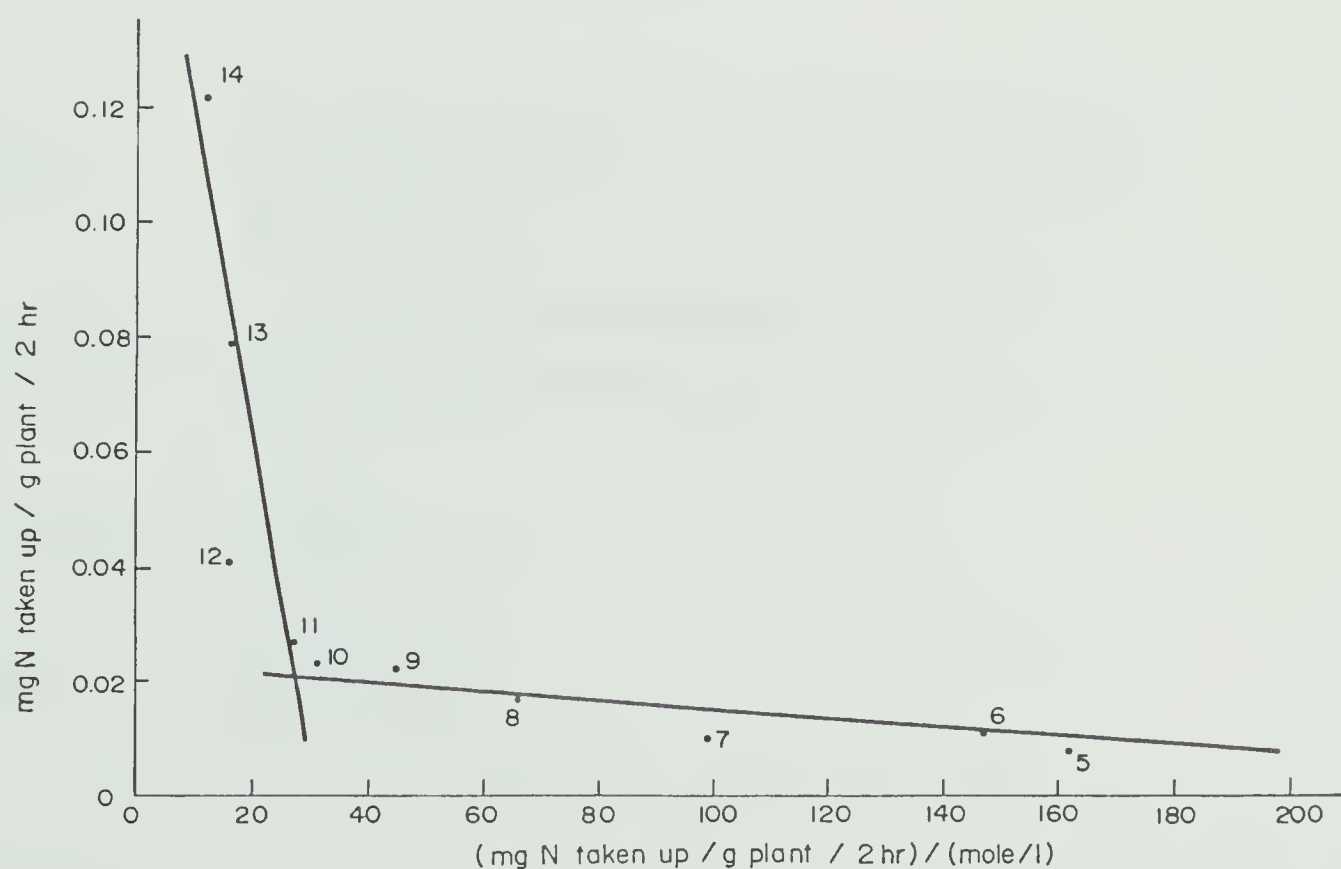


FIGURE 4. HOFSTEE PLOT OF NITRATE UPTAKE FOR WHEATGRASS AT 79 DAYS USING MEANS





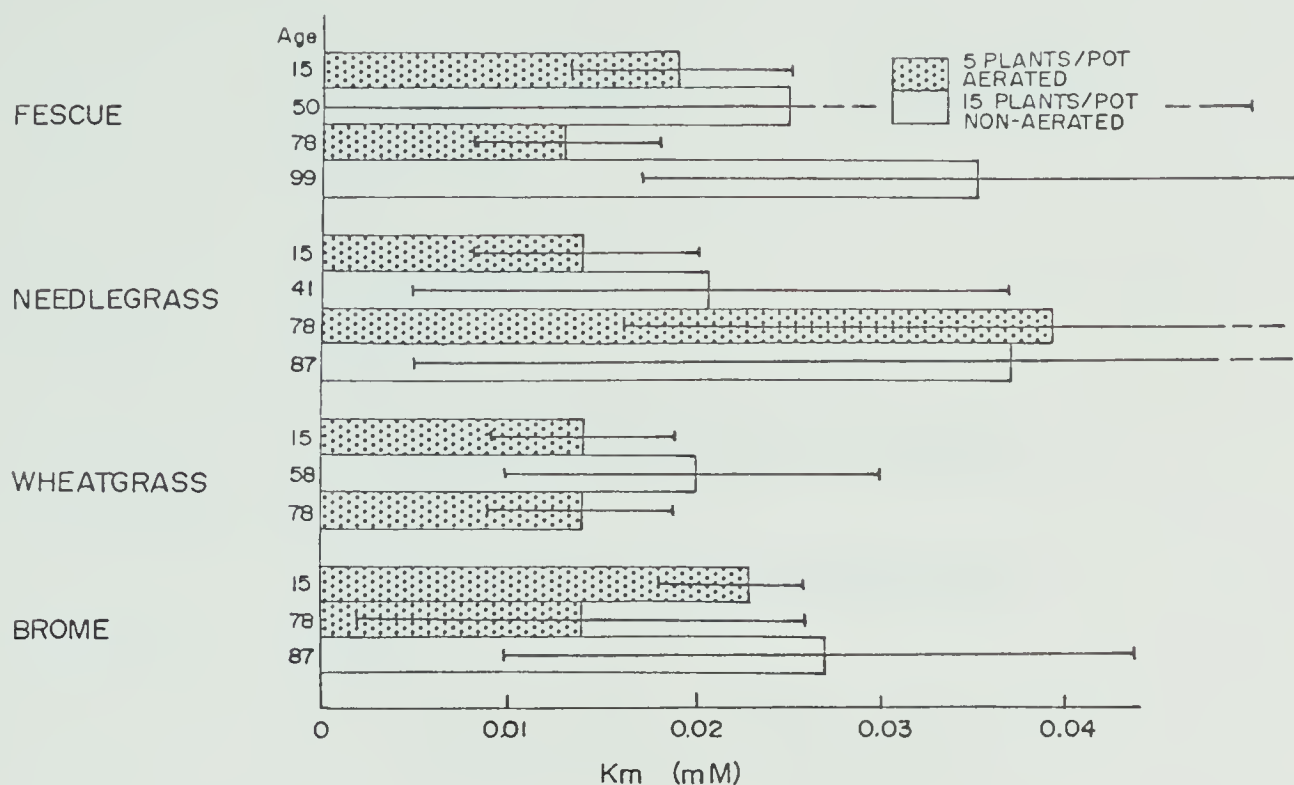


FIGURE 5. COMPARISON OF LOW CONCENTRATION  $K_m$  VALUES FROM AERATED AND NON-AERATED  $NH_4$  UPTAKE SOLUTIONS

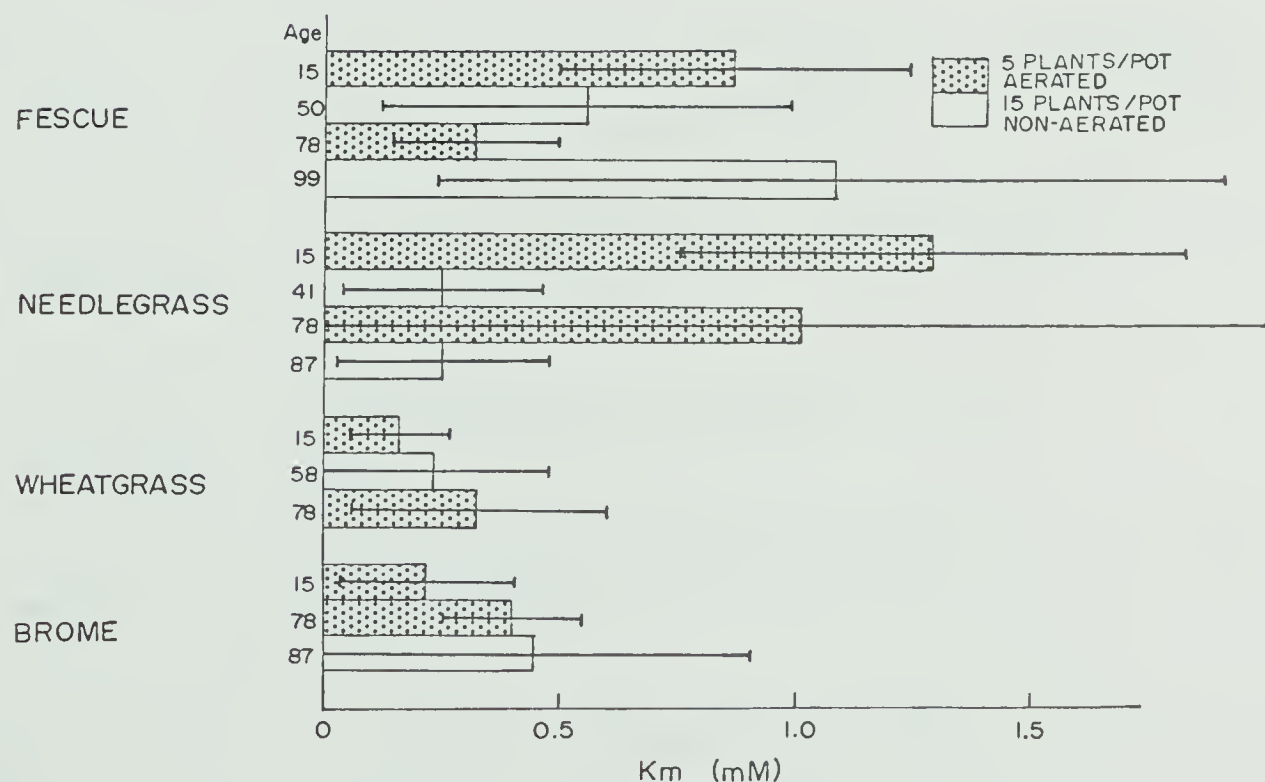


FIGURE 6. COMPARISON OF CORRECTED HIGH CONCENTRATION  $K_m$  VALUES FROM AERATED AND NON-AERATED  $NH_4$  UPTAKE SOLUTIONS



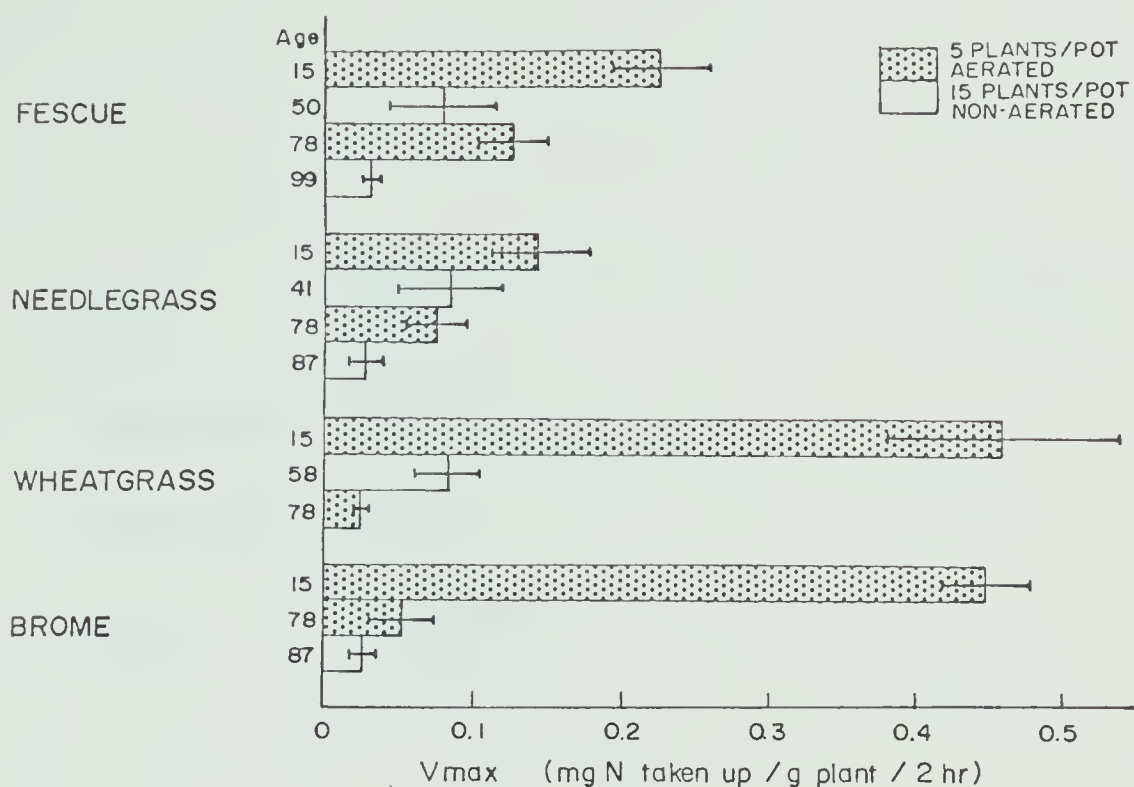


FIGURE 7. COMPARISON OF LOW CONCENTRATION  $V_{max}$  VALUES FROM AERATED AND NON-AERATED  $NH_4$  UPTAKE SOLUTIONS

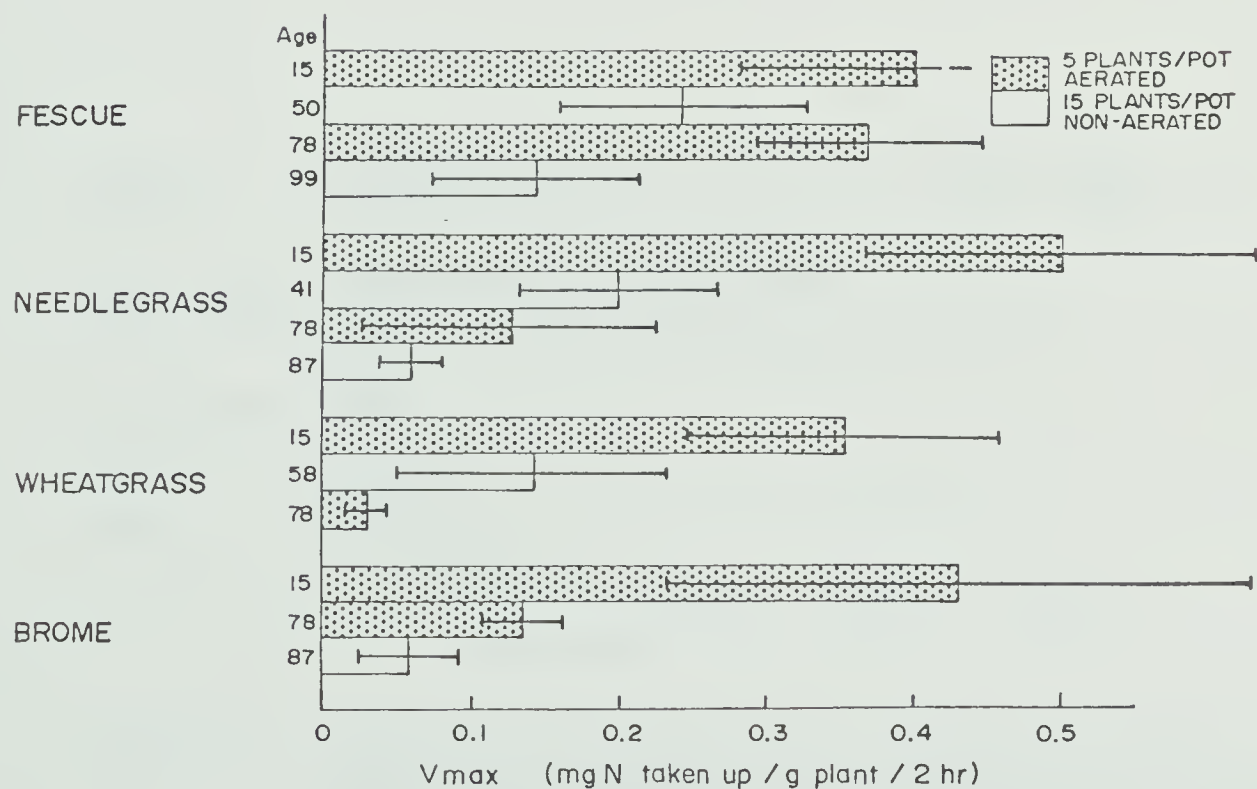


FIGURE 8. COMPARISON OF CORRECTED HIGH CONCENTRATION  $V_{max}$  VALUES FROM AERATED AND NON-AERATED  $NH_4$  UPTAKE SOLUTIONS



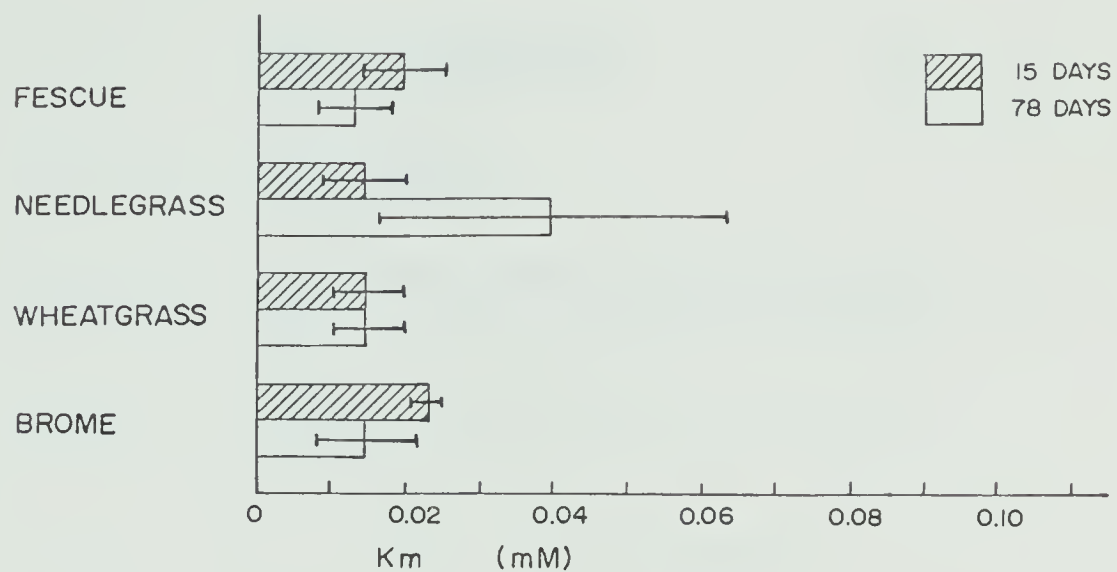


FIGURE 9. MICHAELIS CONSTANTS FOR AMMONIUM UPTAKE OVER THE LOW CONCENTRATION RANGE

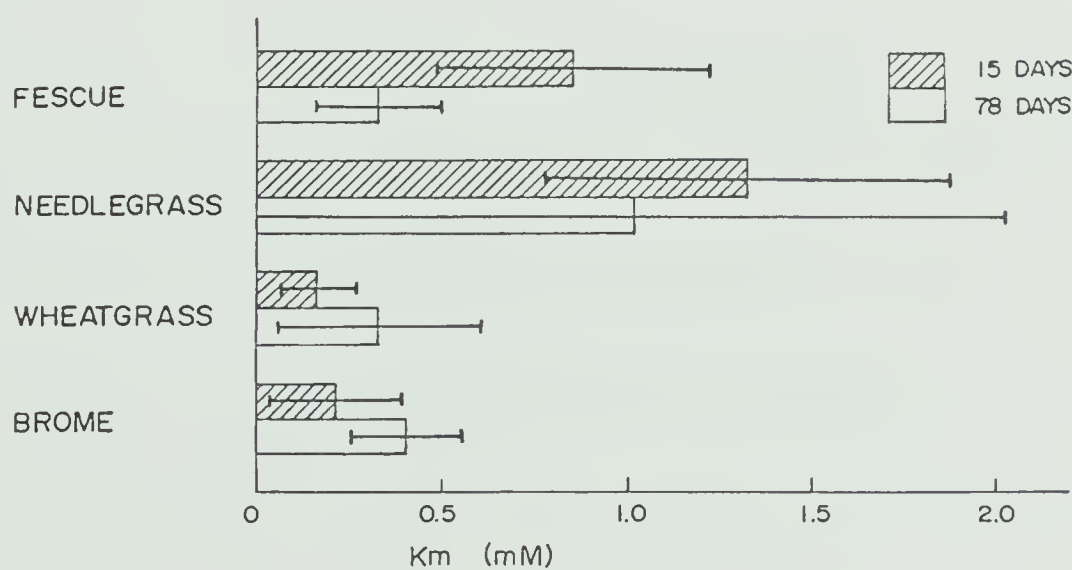


FIGURE 10. MICHAELIS CONSTANTS FOR AMMONIUM UPTAKE OVER THE CORRECTED HIGH CONCENTRATION RANGE



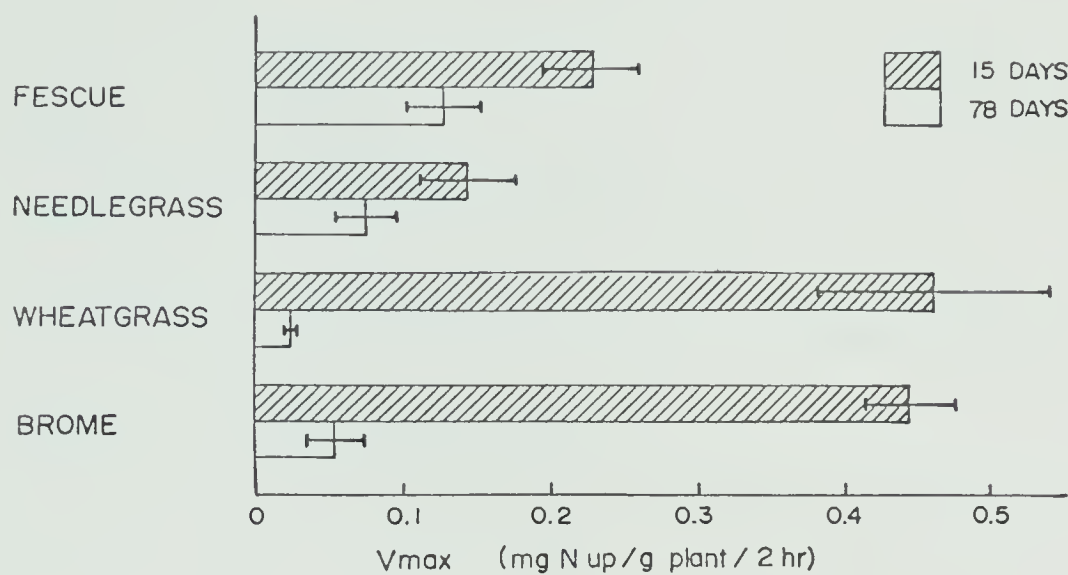


FIGURE 11. MAXIMUM UPTAKE RATES FOR AMMONIUM OVER THE LOW CONCENTRATION RANGE

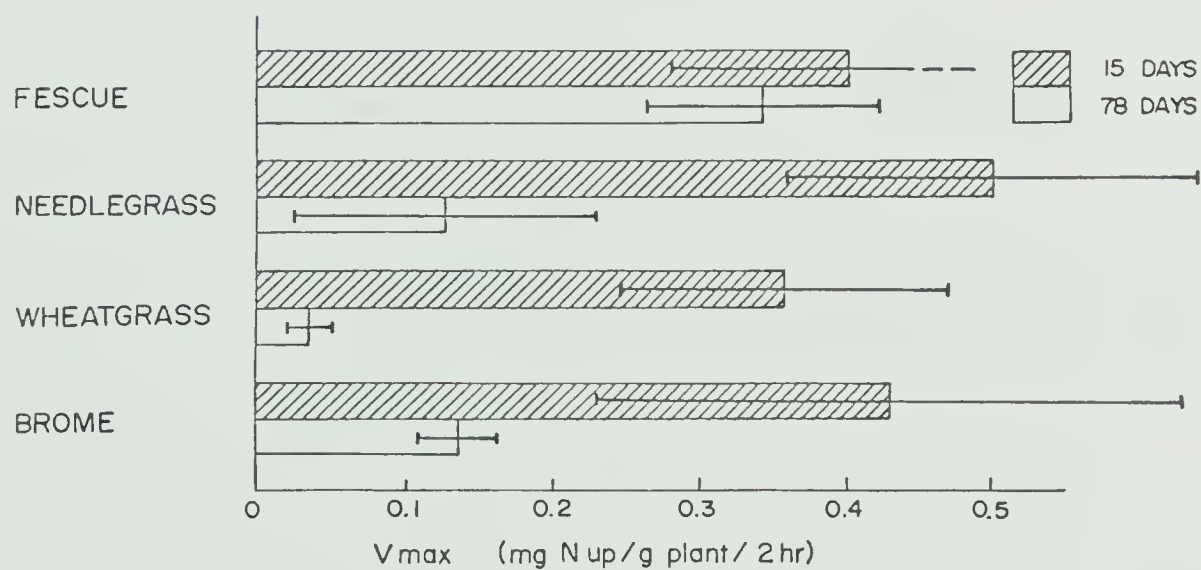


FIGURE 12. MAXIMUM UPTAKE RATES FOR AMMONIUM OVER THE CORRECTED HIGH CONCENTRATION RANGE





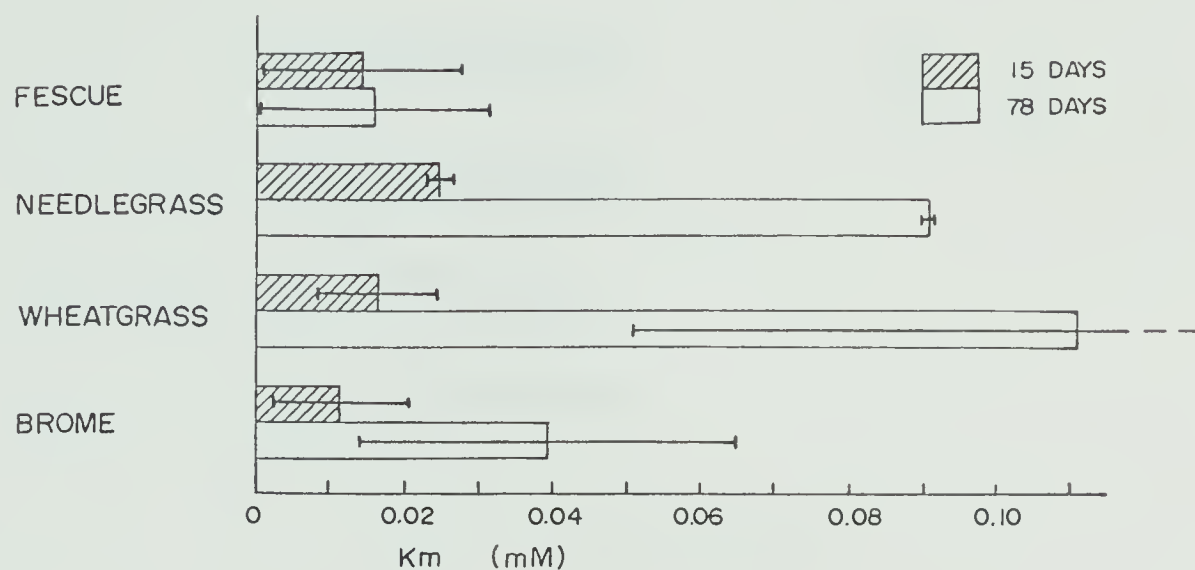


FIGURE 13. MICHAELIS CONSTANTS FOR NITRATE UPTAKE OVER THE LOW CONCENTRATION RANGE

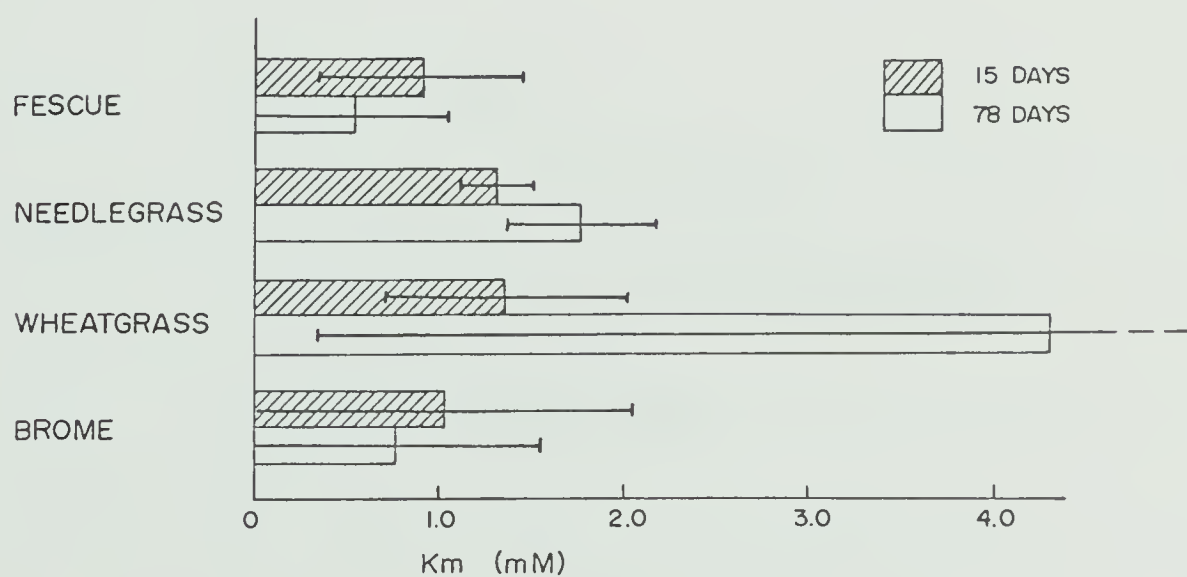


FIGURE 14. MICHAELIS CONSTANTS FOR NITRATE UPTAKE OVER THE CORRECTED HIGH CONCENTRATION RANGE



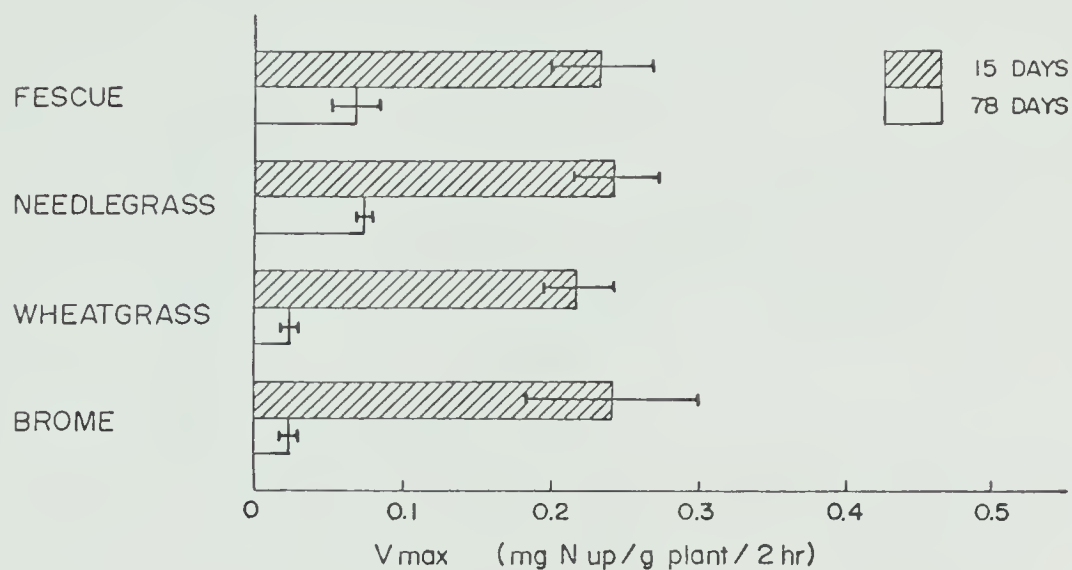


FIGURE 15. MAXIMUM UPTAKE RATES FOR NITRATE OVER THE LOW CONCENTRATION RANGE

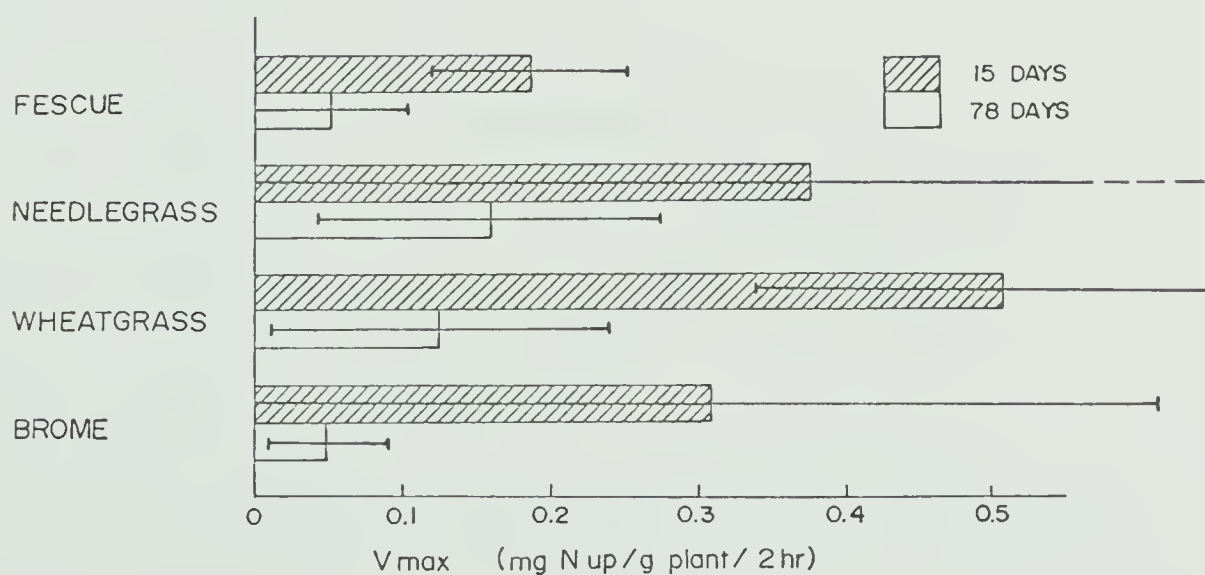


FIGURE 16. MAXIMUM UPTAKE RATES FOR NITRATE OVER THE CORRECTED HIGH CONCENTRATION RANGE



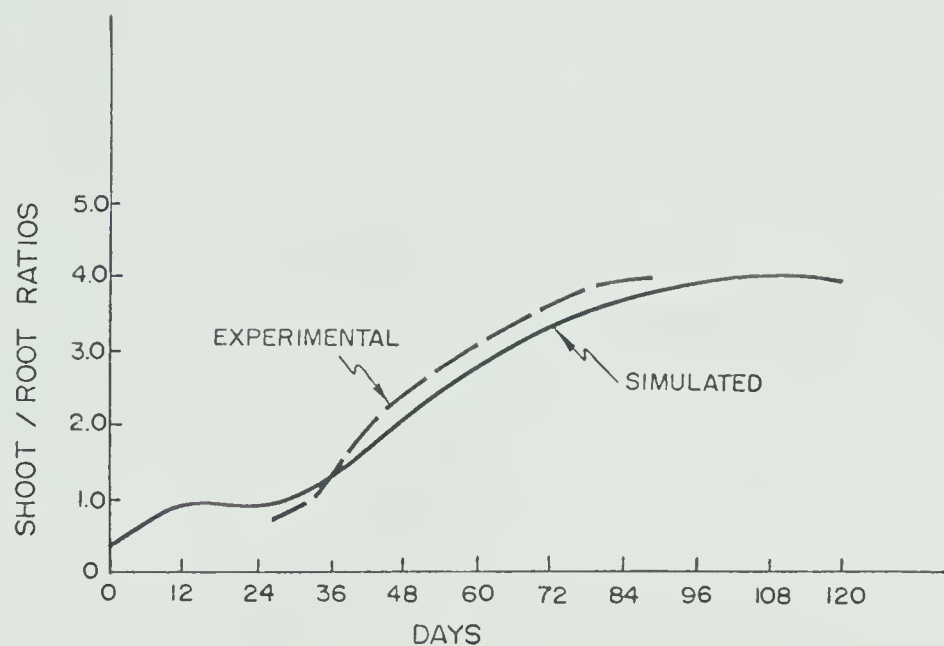


FIGURE 17. COMPARISON OF SIMULATED AND EXPERIMENTAL SHOOT/ROOT RATIOS FOR BROME

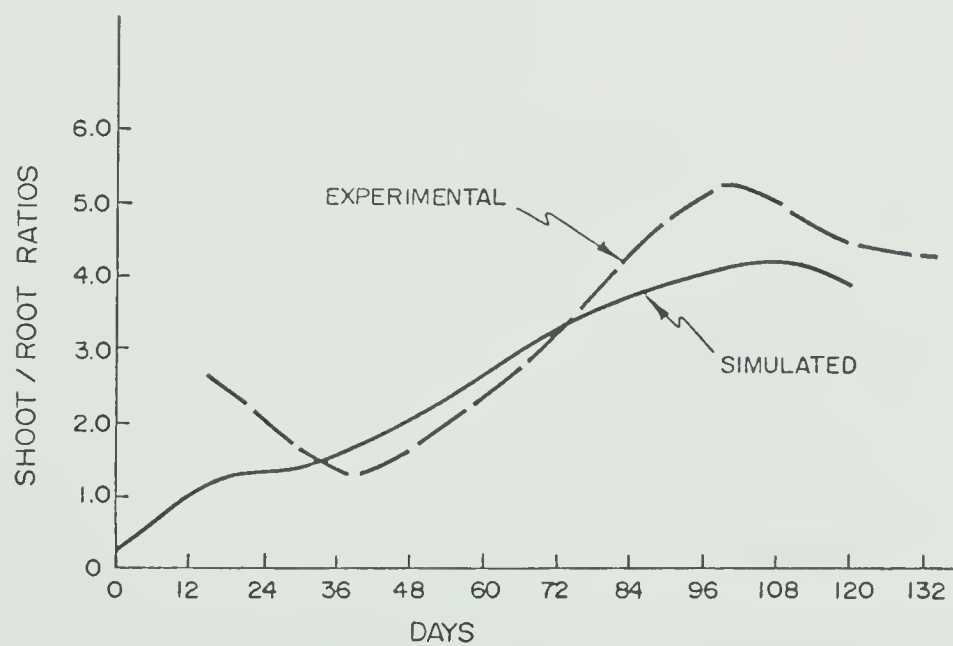


FIGURE 18. COMPARISON OF SIMULATED AND EXPERIMENTAL SHOOT/ROOT RATIOS FOR FESCUE



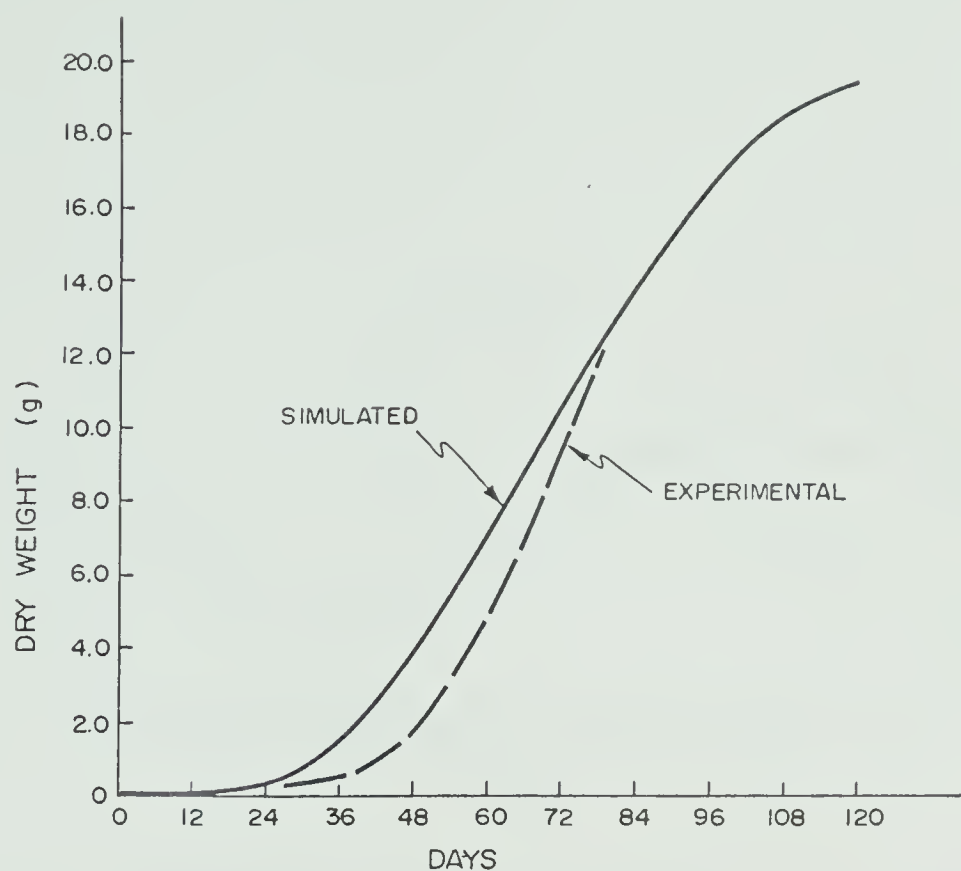


FIGURE 19. COMPARISON OF SIMULATED AND EXPERIMENTAL DRY WEIGHTS FOR BROME

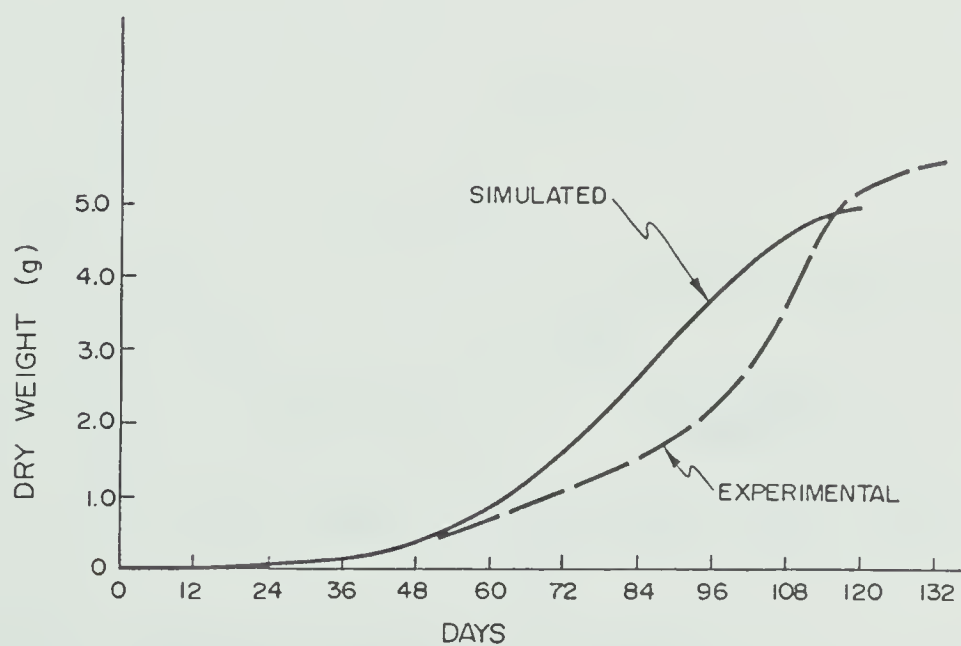


FIGURE 20. COMPARISON OF SIMULATED AND EXPERIMENTAL DRY WEIGHTS FOR FESCUE





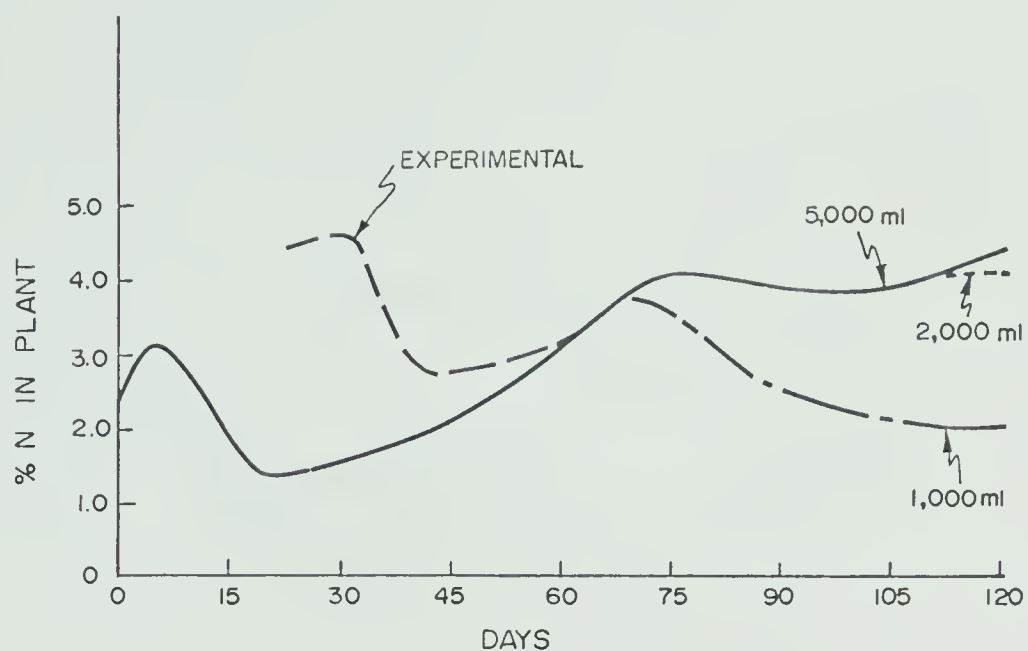


FIGURE 21. NITROGEN CONTENT OF BROME  
AT VARIOUS SOLUTION VOLUMES WITH 120ppm SOIL N

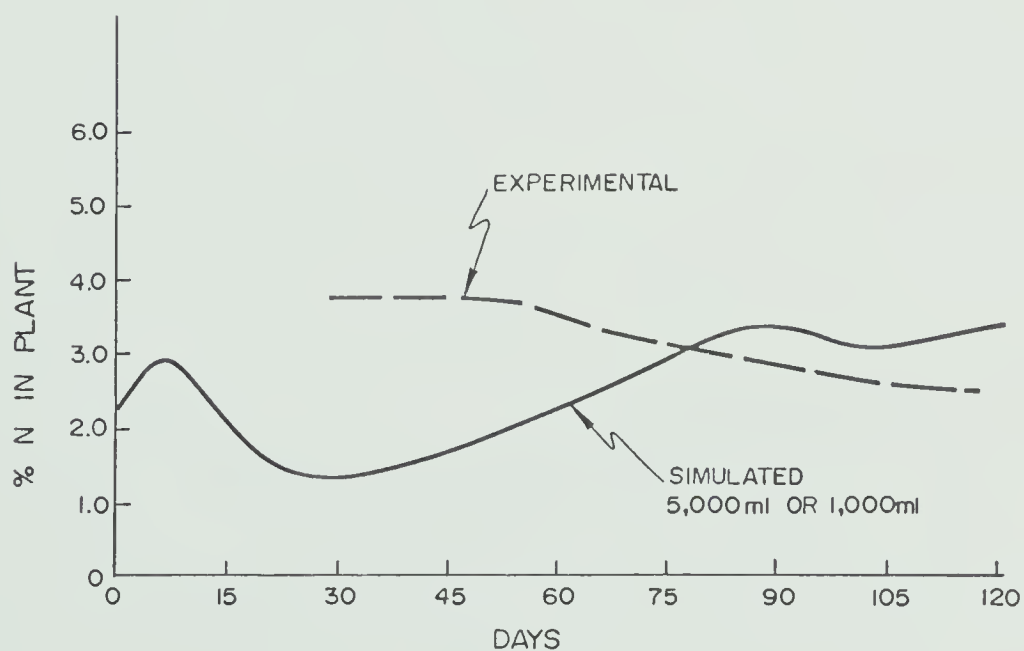


FIGURE 22. NITROGEN CONTENT OF FESCUE  
AT VARIOUS SOLUTION VOLUMES WITH 120ppm SOIL N



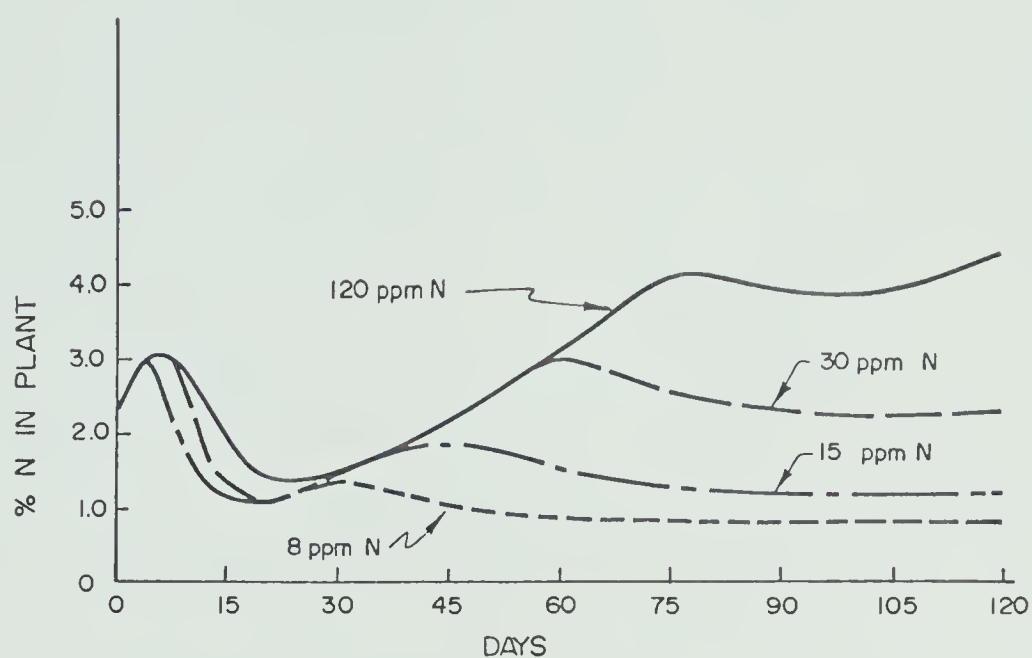


FIGURE 23. NITROGEN CONTENT OF BROME WITH VARYING LEVELS OF SOIL N AND 5,000 ml SOLUTION VOLUME

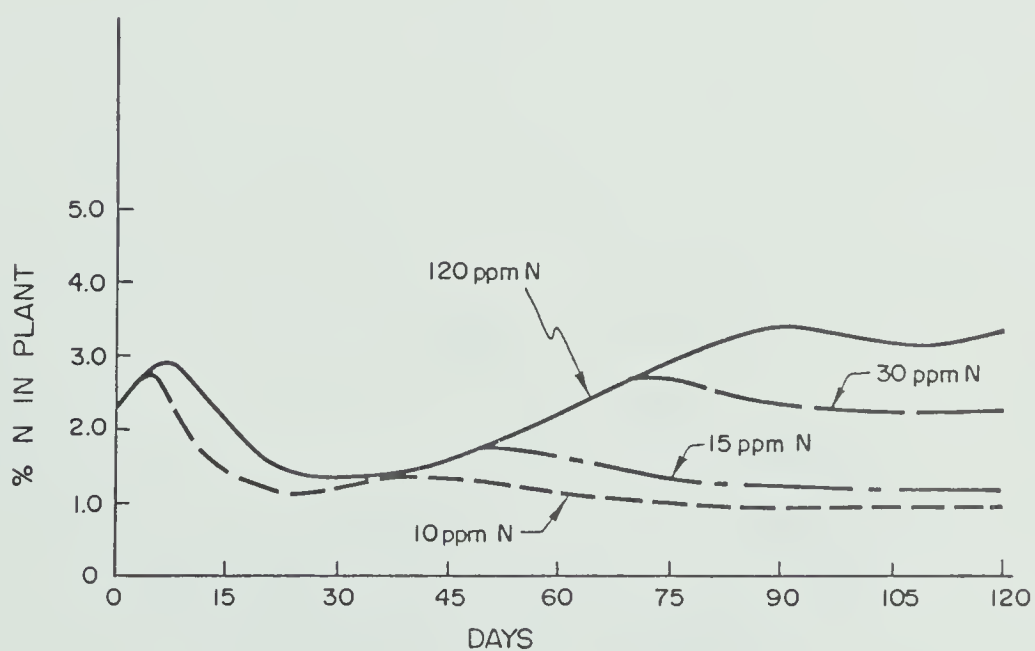


FIGURE 24. NITROGEN CONTENT OF FESCUE WITH VARYING LEVELS OF SOIL N AT 5,000ml SOLUTION VOLUME



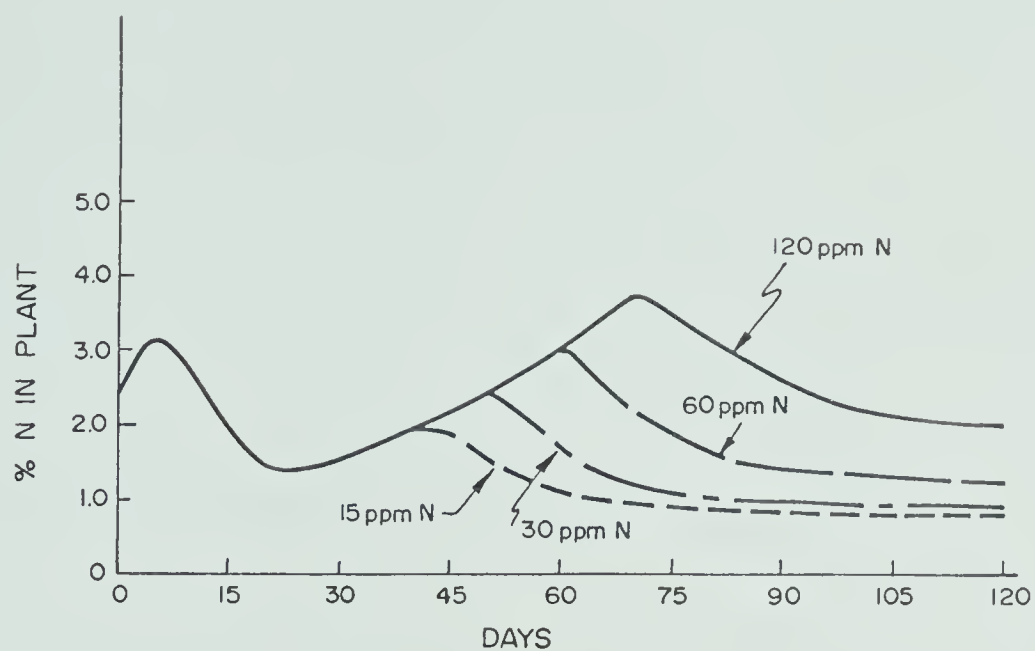


FIGURE 25. NITROGEN CONTENT OF BROME WITH VARYING SOIL N AND SOLUTION VOLUME OF 1,000 ml

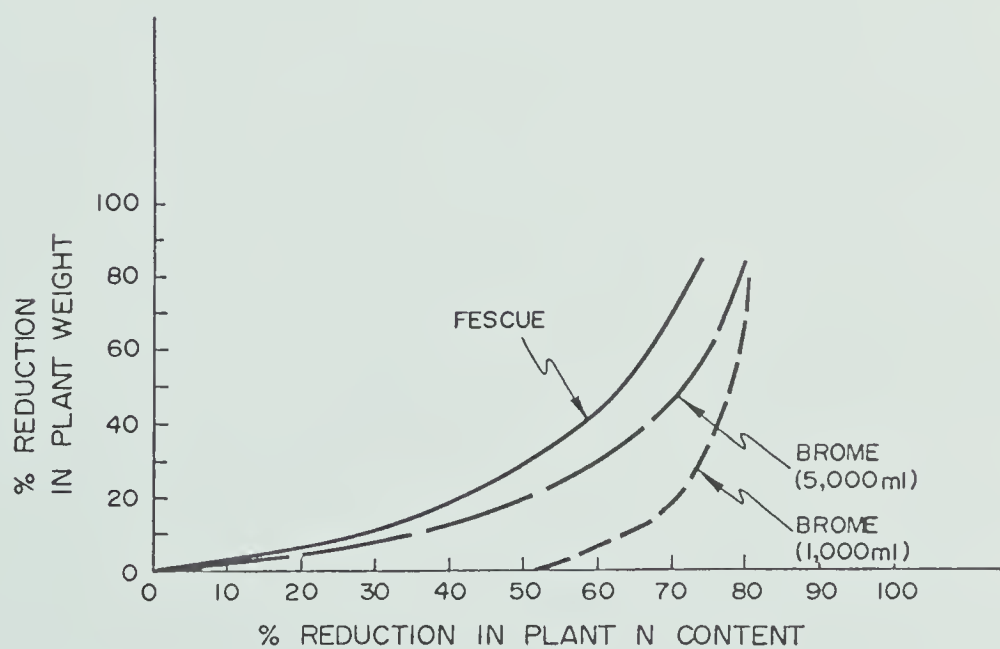


FIGURE 26. RELATIONSHIP BETWEEN REDUCTION IN PLANT WEIGHT AND PLANT N CONTENT



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APPENDICES





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## Appendices

### A. Physical Properties of Sand Medium



Table A-1. Bulk Density of Sand

	Rep 1	Rep 2
Wt. of 100 ml cylinder and sand	287.00	287.64
Wt. of 100 ml cylinder	128.09	127.54
Wt. of sand	159.09	160.10
Bulk Density=Weight/Volume (g/cm <sup>3</sup> )	1.59	1.60

Table A-2. Porosity of Sand and Field Capacity After Draining 1/2 Hour

	Rep 1	Rep 2
Wt. of pot plus wet sand	7150.0	7049.0
Wt. of pot plus dry sand	5875.0	5850.0
Wt. of water	1275.0	1199.0
Percent water = (wet-dry)/dry	21.7	20.1

Porosity =  $(1 - (\text{bulk density} / \text{particle density})) \times 100 = 40\%$   
 where: particle density = 2.65 g/cm<sup>3</sup>



Table A-3. Saturated Hydraulic Conductivity of Sand

		Rep 1	Rep 2	Rep 3
Length of soil column (cm)	L	5.3	6.6	5.3
Diameter of column (cm)		4.5	4.5	4.5
Area of soil column (cm <sup>2</sup> )	A	15.9	15.9	15.9
Hydraulic head (cm)	h	12.6	14.0	12.6

Hydraulic conductivity  $K = (L/Ah)(Q/t)$   
 where:  $Q$  = volume (ml),  $t$  = time (s),  
 $K$  = cm/s

Sample 1			Sample 2			Sample 3		
t	Q	K	t	Q	K	t	Q	K
300	225	0.020	300	192	0.019	300	220	0.020
300	214	0.019	300	187	0.019	300	218	0.019
300	216	0.019	300	194	0.019	300	214	0.019

$$K \text{ (cm/h)} = 0.019 \times 3600 = 68.4$$

Table A-4. Particle Size Distribution of Sand

Mesh Size	Diameter (mm)	% of Sample Passing Mesh		
		Rep 1	Rep 2	Rep 3
18	1.000	100.00	99.91	100.00
35	0.500	99.54	99.55	99.60
60	0.250	30.34	31.81	31.94
140	0.105	0.24	0.44	0.31
270	0.053	0.12	0.20	0.07
Bag	Silt	0.0	0.0	0.0



## B. Preparation of Uptake Solutions





Table B-1. Ammonium Uptake Solution

The stock solution of 0.025 M  $(\text{NH}_4)_2\text{SO}_4$  was equivalent to 0.05 M  $\text{NH}_4$ . The enrichment of excess  $^{15}\text{N}$  was variable, between 30% and 33% depending on source of  $(^{15}\text{NH}_4)_2\text{SO}_4$ .

Concentration (mM)	ml/l of stock Required
0.0025	0.05
0.005	0.10
0.0075	0.15
0.01	0.20
0.025	0.50
0.05	1.00
0.075	1.50
0.10	2.00
0.25	5.00
0.50	10.00
0.75	15.00
1.00	20.00
2.50	50.00
5.00	100.00

Preparation of Stock Solution eg. To 3.0 g  $(^{15}\text{NH}_4)_2\text{SO}_4$  at 30.0 atom % excess  $^{15}\text{N}$  add 907.9 ml water to get 0.025 M  $(\text{NH}_4)_2\text{SO}_4$



Table B-2. Nitrate Uptake Solution

The stock solution of 0.025 M  $\text{Ca}(\text{NO}_3)_2$  was equivalent to 0.05 M  $\text{NO}_3^-$ . The enrichment of excess  $^{15}\text{N}$  was variable, between 30 and 36%, depending on source of  $\text{Ca}(^{15}\text{NO}_3)_2$ .

Concentration (mM)	ml/l of stock Required
0.005	0.10
0.0075	0.15
0.01	0.20
0.025	0.50
0.05	1.00
0.075	1.50
0.10	2.00
0.25	5.00
0.50	10.00
0.75	15.00
1.00	20.00
2.50	50.00
5.00	100.00
10.00	200.00

Preparation of Stock Solution eg. To 5.0 g  $\text{Ca}(^{15}\text{NO}_3)_2$  at 35.0 atom % excess  $^{15}\text{N}$  add 847 ml water to get 0.025 M  $\text{Ca}(\text{NO}_3)_2$



### C. Sample Calculations



Table C-1. Percent Total Nitrogen in Plant

$$\% \text{ Total N} = (\text{ml H}_2\text{SO}_4 \text{ titre} - \text{ml H}_2\text{SO}_4 \text{ blank}) \times (\text{Normality of Acid})(1.4) / \text{Weight of sample (g)}$$

Table C-2. Uptake Calculations

Hofstee Plot Parameters  $v$  and  $v/S$

$$v = (\% \text{ excess } ^{15}\text{N} \text{ in sample} / \% \text{ excess } ^{15}\text{N} \text{ in solution}) \times \% \text{ total N in plant} \times 10$$

where:  $v$  = uptake velocity in mg N taken up/g plant/2 h  
and 1% N in plant = 10 mg N/g plant

$$v/S = (\text{mg N taken up/g plant/2 h}) / (\text{mol/l})$$

where:  $S$  = substrate concentration of ammonium or nitrate in mol/l

Table C-3. Calculation of % Excess  $^{15}\text{N}$  from Mass Spectrometer

$$\% \text{ Abundance} = 100 / ((272((\text{Ratio Ref} + \text{Read. Ref}) / (\text{Ratio Sam} + \text{Read Sam} + \text{Offset}))) + 1)$$

$$\% \text{ Excess } ^{15}\text{N} = \% \text{ Abundance} - 0.3675^1$$

where Ref = Reference and Sam = Sample  
<sup>1</sup>the natural abundance of  $^{15}\text{N}$  in the atmosphere is normally taken as 0.367647 %, not 0.3675 % as used in these calculations





D. Ammonium Uptake Kinetic Data for Experiments Using  
Ammonium Plus Nutrient Solution



Table D-1. Ammonium Uptake Kinetic Data for Alpine Sheep Fescue After 15 Days (31.3% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1		.0104	4.85	.0174	.0270	10784.66
2	2.5E-6	.0113	3.59	.0446	.0512	20461.85
3		.0078	4.49	.0243	.0349	13943.39
4		.0115	3.83	.0386	.0472	9446.52
5	5.0E-6	.0061	4.82	.0243	.0374	7484.09
6		.0158	3.37	.0000	.0000	.00
7		.0114	4.32	.0551	.0760	10139.81
8	7.5E-6	.0083	6.04	.0273	.0527	7024.15
9		.0095	4.32	.0675	.0932	12421.73
10		.0120	4.12	.0582	.0766	7660.83
11	1.0E-5	.0086	4.41	.0639	.0900	9003.16
12		.0105	4.93	.0312	.0491	4914.25
13		.0115	4.94	.0426	.0672	2689.38
14	2.5E-5	.0123	4.06	.1222	.1585	6340.35
15		.0096	4.20	.1299	.1743	6972.27
16		.0153	4.36	.1498	.2087	4173.34
17	5.0E-5	.0079	4.78	.0918	.1402	2803.86
18		.0055	3.95	.0905	.1142	2284.19
19		.0146	4.52	.1546	.2233	2976.75
20	7.5E-5	.0056	4.38	.0923	.1292	1722.15
21		.0088	4.50	.1614	.2320	3093.93
22		.0148	4.10	.2227	.2917	2917.16
23	1.0E-4	.0065	3.81	.1030	.1254	1253.77
24		.0072	4.53	.1255	.1816	1816.34
25		.0112	4.64	.1281	.1899	759.60
26	2.5E-4	.0082	6.33	.1071	.2166	866.38
27		.0070	4.48	.1462	.2093	837.03
28		.0136	4.30	.2239	.3076	615.19
29	5.0E-4	.0089	3.38	.1555	.1679	335.84
30		.0058	4.92	.1303	.2048	409.63
31		.0125	4.23	.2602	.3516	468.86
32	7.5E-4	.0168	2.03	.1601	.1038	138.45
33		.0063	4.60	.2513	.3693	492.43
34		.0143	4.39	.2655	.3724	372.38
35	1.0E-3	.0067	4.83	.2206	.3404	340.41
36		.0069	4.54	.2479	.3596	359.57
37		.0118	4.35	.3658	.5084	203.35
38	2.5E-3	.0056	4.60	.2324	.3415	136.62
39		.0091	4.38	.3540	.4954	198.15
40		.0079	4.61	.3818	.5623	112.47
41	5.0E-3	.0074	4.92	.3528	.5546	110.91
42		.0080	4.74	.3383	.5123	102.46



Table D-2. Ammonium Uptake Kinetic Data for Alpine Sheep Fescue After 50 Days (32.2% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis	
1		.2659	1.43	.0175	.0078	3108.70	
2	2.5E-6	.2388	1.69	.0152	.0080	3191.06	
3		.2437	1.64	.0145	.0074	2954.04	
4		.1897	1.62	.0260	.0131	2616.15	
5	5.0E-6	.2669	1.42	.0294	.0130	2593.04	
6		.3056	1.44	.0307	.0137	2745.84	
7		.2713	1.53	.0359	.0171	2274.41	
8	7.5E-6	.2257	1.56	.0417	.0202	2693.66	
9		.2115	2.18	.0317	.0215	2861.53	
10		.3815	1.27	.0348	.0137	1372.55	
11	1.0E-5	.2570	1.50	.0000	.0000	.00	
12		.2863	1.33	.0478	.0197	1974.35	
13		.2462	1.50	.0000	.0000	.00	
14	2.5E-5	.2200	1.32	.0562	.0230	921.54	
15		.2493	1.61	.0649	.0324	1298.00	
16		.2846	1.76	.0822	.0449	898.58	
17	5.0E-5	.2988	1.50	.0915	.0426	852.48	
18		.1827	1.84	.1032	.0590	1179.43	
19		.1207	2.38	.1057	.0781	1041.68	
20	7.5E-5	.2798	1.62	.1791	.0901	1201.42	
21		.2424	1.88	.1177	.0687	916.26	
22		.2629	1.49	.1842	.0852	852.35	
23	1.0E-4	.2766	1.24	.1385	.0533	533.35	
24		.2593	1.66	.1310	.0675	675.34	
25		.2603	1.44	.1981	.0886	354.37	
26	2.5E-4	.2447	1.65	.2533	.1298	519.19	
27		.2190	1.69	.4298	.2256	902.31	
28		.1930	1.44	.2542	.1137	227.36	
29	5.0E-4	.2740	1.66	.3886	.2003	400.67	
30		.1679	1.39	.2502	.1080	216.01	
31		.2579	1.50	.0000	.0000	.00	
32	7.5E-4	.2646	1.67	.4689	.2432	324.25	
33		.2345	1.53	.3130	.1487	198.30	
34		.2934	1.46	.3654	.1657	165.68	
35	1.0E-3	.1849	1.26	.5193	.2032	203.20	
36		.1856	1.50	.0000	.0000	.00	
37		.2611	1.40	.5149	.2239	89.55	
38	2.5E-3	.2244	1.40	.6431	.2796	111.84	
39		.3001	1.45	.5712	.2572	102.89	
40		.2101	1.40	.6880	.2991	59.83	
41	5.0E-3	.2568	1.79	.5837	.3245	64.90	
42		.2505	1.49	.5899	.2730	54.59	



Table D-3. Ammonium Uptake Kinetic Data for Alpine Sheep Fescue After 78 Days (30.1% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis	
1A		1.6732	1.85	.1229	.0755	30214.62	
1B		1.6732	1.83	.1170	.0711	28453.16	
2A	2.5E-6	1.6085	2.21	.0711	.0522	20881.20	
2B		1.6085	2.42	.0676	.0543	21739.80	
3A		2.0322	1.24	.0624	.0257	10282.52	
3B		2.0322	1.15	.0589	.0225	9001.33	
4A		1.4313	1.58	.0939	.0493	9857.94	
4B		1.4313	1.82	.0839	.0507	10146.05	
5A	5.0E-6	2.4885	1.11	.0562	.0207	4144.98	
5B		2.4885	1.42	.0548	.0259	5170.50	
6A		2.3160	1.04	.0527	.0182	3641.73	
6B		2.3160	1.28	.0530	.0225	4507.64	
7A		.9065	1.89	.1300	.0816	10883.72	
7B		.9065	1.82	.1326	.0802	10690.23	
8A	7.5E-6	1.6759	1.60	.0953	.0507	6754.37	
8B		1.6759	1.54	.0994	.0509	6780.78	
9A		2.7487	1.29	.0606	.0260	3462.86	
9B		2.7487	1.53	.0553	.0281	3747.91	
10A		1.2003	1.79	.1567	.0932	9318.70	
10B		1.2003	1.84	.1575	.0963	9627.91	
11A	1.0E-5	1.3728	1.13	.1089	.0409	4088.27	
11B		1.3728	1.29	.1005	.0431	4307.14	
12A		1.8119	1.44	.0588	.0281	2813.02	
12B		1.8119	1.64	.0573	.0312	3121.99	
13A		2.0007	1.22	.1019	.0413	1652.07	
13B		2.0007	1.41	.1049	.0491	1965.57	
14A	2.5E-5	1.5796	1.41	.1239	.0580	2321.58	
14B		1.5796	1.53	.1084	.0551	2204.01	
15A		2.5605	1.23	.1192	.0487	1948.39	
15B		2.5605	1.23	.1112	.0454	1817.62	
16A		1.6418	1.65	.1658	.0909	1817.74	
16B		1.6418	1.75	.1500	.0872	1744.19	
17A	5.0E-5	1.1810	2.55	.1571	.1331	2661.83	
17B		1.1810	2.61	.1702	.1476	2951.64	
18A		2.1898	1.26	.1544	.0646	1292.65	
18B		2.1898	1.37	.1590	.0724	1447.38	
19A		2.0049	1.70	.2719	.1536	2047.53	
19B		2.0049	1.55	.2684	.1382	1842.83	
20A	7.5E-5	2.4188	1.21	.1982	.0797	1062.33	
20B		2.4188	1.33	.2026	.0895	1193.61	





## Hofstee Plot Parameters

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
21A		1.8018	1.84	.1956	.1196	1594.26
21B		1.8018	1.61	.1828	.0978	1303.69
22A		3.2578	1.21	.3259	.1310	1310.10
22B		3.2578	.94	.3337	.1042	1042.12
23A	1.0E-4	2.4649	1.63	.2138	.1158	1157.79
23B		2.4649	1.33	.2132	.0942	942.05
24A		2.3797	1.28	.2550	.1084	1084.39
24B		2.3797	1.46	.2345	.1137	1137.44
25A		2.2739	1.68	.4311	.2406	962.46
25B		2.2739	1.37	.4624	.2105	841.84
26A	2.5E-4	2.9248	1.59	.3606	.1905	761.93
26B		2.9248	1.75	.3453	.2008	803.02
27A		1.8525	1.53	.3161	.1607	642.70
27B		1.8525	1.47	.3552	.1735	693.88
28A		1.4714	1.49	.4970	.2460	492.05
28B		1.4714	1.49	.5290	.2619	523.73
29A	5.0E-4	1.6578	1.42	.4143	.1955	390.90
29B		1.6578	1.98	.4657	.3063	612.68
30A		1.7398	1.23	.3794	.1550	310.07
30B		1.7398	1.33	.4121	.1821	364.18
31A		1.2676	1.69	.6685	.3753	500.45
31B		1.2676	1.72	.6776	.3872	516.27
32A	7.5E-4	2.6252	1.87	.4222	.2623	349.73
32B		2.6252	1.53	.4437	.2255	300.71
33A		1.0853	1.50	.6504	.3241	432.16
33B		1.0853	1.78	.7005	.4142	552.33
34A		2.7308	1.62	.7868	.4235	423.46
34B		2.7308	1.95	.6442	.4173	417.34
35A	1.0E-3	1.8992	2.24	.7722	.5747	574.66
35B		1.8992	1.60	.7006	.3724	372.41
36A		1.7723	1.52	.6571	.3318	331.82
36B		1.7723	.92	.6239	.1907	190.69
37A		2.1759	1.44	.7220	.3454	138.16
37B		2.1759	1.92	.7939	.5064	202.56
38A	2.5E-3	2.7977	1.43	.6572	.3122	124.89
38B		2.7977	1.35	.7671	.3440	137.62
39A		.7993	1.59	.7235	.3822	152.87
39B		.7993	1.35	.7145	.3205	128.18
40A		3.0470	1.80	.7947	.4752	95.05
40B		3.0470	2.00	.8105	.5385	107.71
41A	5.0E-3	1.8826	1.86	.7301	.4512	90.23
41B		1.8826	2.20	.7214	.5273	105.45
42A		2.9962	1.39	.7911	.3653	73.07
42B		2.9962	2.27	.7845	.5916	118.33



Table D-4. Ammonium Uptake Kinetic Data for Alpine Sheep Fescue After 99 Days (31.0% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1		2.6427	1.39	.0155	.0069	2780.00
2	2.5E-6	1.4323	2.10	.0058	.0039	1571.61
3		1.3308	1.58	.0152	.0077	3098.84
4		1.5745	1.77	.0154	.0088	1758.58
5	5.0E-6	2.5082	1.17	.0334	.0126	2521.16
6		1.6728	1.89	.0078	.0048	951.10
7		2.6442	1.63	.0089	.0047	623.96
8	7.5E-6	2.2456	1.48	.0173	.0083	1101.25
9		1.3330	1.88	.0094	.0057	760.09
10		1.5766	1.78	.0165	.0095	947.42
11	1.0E-5	1.6988	1.71	.0095	.0052	524.03
12		1.2266	2.10	.0076	.0051	514.84
13		1.1928	1.43	.0406	.0187	749.14
14	2.5E-5	1.9204	1.88	.0135	.0082	327.48
15		1.5470	1.82	.0259	.0152	608.23
16		1.9160	1.45	.0394	.0184	368.58
17	5.0E-5	1.9849	1.64	.0248	.0131	262.40
18		1.2584	2.07	.0313	.0209	418.01
19		2.5109	1.50	.0677	.0328	436.77
20	7.5E-5	1.9082	1.57	.0634	.0321	428.12
21		1.9581	2.15	.0245	.0170	226.56
22		2.0961	2.07	.0479	.0320	319.85
23	1.0E-4	1.3053	1.73	.0375	.0209	209.27
24		1.4869	1.94	.0215	.0135	134.55
25		1.0179	1.56	.0761	.0383	153.18
26	2.5E-4	1.4427	1.80	.0448	.0260	104.05
27		1.8505	1.83	.0498	.0294	117.59
28		1.8126	1.94	.0813	.0509	101.76
29	5.0E-4	1.7168	2.21	.0584	.0416	83.27
30		1.3362	1.83	.0752	.0444	88.78
31		1.7896	2.01	.0828	.0537	71.58
32	7.5E-4	1.3868	1.99	.0607	.0390	51.95
33		1.5361	2.00	.0980	.0632	84.30
34		1.5483	1.37	.3095	.1368	136.78
35	1.0E-3	2.2734	1.84	.1277	.0758	75.80
36		1.3197	1.83	.0780	.0460	46.05
37		1.7390	1.32	.2636	.1122	44.90
38	2.5E-3	2.0694	1.63	.2399	.1261	50.46
39		1.6456	1.52	.2408	.1181	47.23
40		1.5800	1.51	.3459	.1685	33.70
41	5.0E-3	1.7819	2.10	.2059	.1395	27.90
42		2.3142	1.72	.2453	.1361	27.22



Table D-5. Ammonium Uptake Kinetic Data for Columbia Needlegrass After 15 Days (31.0% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis	
1		.0269	3.58	.0282	.0326	13026.58	
2	2.5E-6	.0309	3.31	.0259	.0277	11061.81	
3		.0292	3.26	.0314	.0330	13208.26	
4		.0333	3.57	.0333	.0383	7669.74	
5	5.0E-6	.0409	3.18	.0344	.0353	7057.55	
6		.0240	3.56	.0423	.0486	9715.35	
7		.0273	3.58	.0418	.0483	6436.30	
8	7.5E-6	.0164	3.58	.0475	.0549	7313.98	
9		.0288	4.59	.0288	.0426	5685.68	
10		.0174	3.94	.0405	.0515	5147.42	
11	1.0E-5	.0333	3.15	.0604	.0614	6137.42	
12		.0307	3.24	.0478	.0500	4995.87	
13		.0259	3.79	.0801	.0979	3917.15	
14	2.5E-5	.0323	3.51	.0684	.0774	3097.86	
15		.0295	3.56	.0640	.0735	2939.87	
16		.0284	3.94	.0855	.1087	2173.35	
17	5.0E-5	.0253	3.98	.0866	.1112	2223.66	
18		.0272	3.86	.0898	.1118	2236.31	
19		.0255	3.57	.1723	.1984	2645.64	
20	7.5E-5	.0182	3.54	.0793	.0906	1207.41	
21		.0370	3.58	.0920	.1062	1416.60	
22		.0318	3.57	.1280	.1474	1474.06	
23	1.0E-4	.0318	3.74	.1251	.1509	1509.27	
24		.0229	3.61	.1618	.1884	1884.19	
25		.0255	3.95	.1534	.1955	781.85	
26	2.5E-4	.0154	3.64	.1189	.1396	558.45	
27		.0289	3.78	.1179	.1438	575.05	
28		.0194	3.54	.1090	.1245	248.94	
29	5.0E-4	.0275	3.41	.1588	.1747	349.36	
30		.0253	3.62	.1737	.2028	405.67	
31		.0286	3.48	.1943	.2181	290.82	
32	7.5E-4	.0231	3.91	.2065	.2605	347.28	
33		.0352	3.18	.2258	.2316	308.84	
34		.0278	3.20	.3879	.4004	400.41	
35	1.0E-3	.0266	3.47	.2189	.2450	245.03	
36		.0160	3.54	.1863	.2127	212.74	
37		.0241	3.57	.2904	.3344	133.77	
38	2.5E-3	.0326	3.35	.3889	.4203	168.11	
39		.0210	3.57	.3698	.4259	170.35	
40		.0276	3.70	.4317	.5153	103.05	
41	5.0E-3	.0270	3.40	.5297	.5810	116.19	
42		.0234	3.44	.4250	.4716	94.32	



Table D-6. Ammonium Uptake Kinetic Data for Columbia Needlegrass After 41 Days (31.6% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basals
1		.3079	1.47	.0266	.0124	4949.62
2	2.5E-6	.2149	1.44	.0287	.0131	5231.39
3		.2508	1.54	.0329	.0160	6413.42
4		.1751	1.74	.0303	.0167	3336.84
5	5.0E-6	.3051	1.40	.0255	.0113	2259.49
6		.3644	1.73	.0294	.0161	3219.11
7		.3440	1.76	.0516	.0287	3831.90
8	7.5E-6	.1685	1.48	.0359	.0168	2241.86
9		.1085	1.91	.0492	.0297	3965.06
10		.2780	1.57	.0470	.0234	2335.13
11	1.0E-5	.1534	1.60	.0536	.0271	2713.92
12		.1277	1.73	.0499	.0273	2731.87
13		.1884	1.70	.1045	.0562	2248.73
14	2.5E-5	.4521	1.43	.0800	.0362	1448.10
15		.2213	1.56	.1064	.0525	2101.06
16		.2659	1.41	.0922	.0411	822.80
17	5.0E-5	.2104	1.71	.1079	.0584	1167.78
18		.3185	1.50	.0000	.0000	.00
19		.1431	1.65	.1483	.0774	1032.47
20	7.5E-5	.1624	1.36	.1761	.0758	1010.53
21		.2531	1.68	.1552	.0825	1100.15
22		.1201	2.21	.2930	.2049	2049.15
23	1.0E-4	.1254	2.20	.3157	.2198	2197.91
24		.2138	1.92	.3043	.1849	1848.91
25		.2744	1.84	.2429	.1414	565.74
26	2.5E-4	.2277	1.90	.2420	.1455	582.03
27		.1881	1.87	.2352	.1392	556.74
28		.2155	2.06	.2921	.1904	380.84
29	5.0E-4	.1317	1.42	.2883	.1296	259.11
30		.3288	1.91	.2781	.1681	336.18
31		.1420	2.10	.1161	.0772	102.87
32	7.5E-4	.2029	1.86	.1241	.0730	97.39
33		.1989	1.90	.1682	.1011	134.84
34		.1646	1.50	.0000	.0000	.00
35	1.0E-3	.2544	2.19	.3113	.2157	215.74
36		.1557	2.08	.2934	.1931	193.12
37		.3579	1.79	.3595	.2036	81.46
38	2.5E-3	.1576	2.86	.3778	.3419	136.77
39		.2167	1.88	.3900	.2320	92.81
40		.2608	1.48	.5231	.2450	49.00
41	5.0E-3	.1567	2.01	.4920	.3129	62.59
42		.2332	1.81	.5434	.3113	62.25





Table D-7. Ammonium Uptake Kinetic Data for Columbia Needlegrass After 78 Days (30.1% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1A		6.2274	1.42	.0200	.0094	3774.09
1B		6.2274	1.00	.0199	.0066	2644.52
2A	2.5E-6	5.3863	1.41	.0301	.0141	5640.00
2B		5.3863	1.43	.0263	.0125	4997.87
3A		8.5588	1.31	.0400	.0174	6963.46
3B		8.5588	1.42	.0387	.0183	7302.86
4A		4.0033	1.18	.0302	.0118	2367.84
4B		4.0033	1.17	.0293	.0114	2277.81
5A	5.0E-6	6.9789	1.62	.0219	.0118	2357.34
5B		6.9789	1.73	.0230	.0132	2643.85
6A		1.8120	1.91	.0355	.0225	4505.32
6B		1.8120	1.86	.0382	.0236	4721.06
7A		6.6997	1.30	.0418	.0181	2407.09
7B		6.6997	1.26	.0377	.0158	2104.19
8A	7.5E-6	5.5157	1.38	.0394	.0181	2408.50
8B		5.5157	1.21	.0350	.0141	1875.97
9A		3.1503	1.55	.0423	.0218	2904.32
9B		3.1503	1.68	.0371	.0207	2760.93
10A		6.8891	1.34	.0458	.0204	2038.94
10B		6.8891	1.33	.0374	.0165	1652.56
11A	1.0E-5	4.8457	1.05	.0438	.0153	1527.91
11B		4.8457	1.02	.0403	.0137	1365.65
12A		6.7814	1.38	.0318	.0146	1457.94
12B		6.7814	1.29	.0355	.0152	1521.43
13A		5.6921	1.59	.0638	.0337	1348.07
13B		5.6921	1.49	.0566	.0280	1120.72
14A	2.5E-5	5.0217	1.78	.0566	.0335	1338.84
14B		5.0217	1.87	.0499	.0310	1240.04
15A		8.3025	1.53	.0450	.0229	914.95
15B		8.3025	1.48	.0406	.0200	798.51
16A		4.8135	1.15	.1364	.0521	1042.26
16B		4.8135	1.37	.1149	.0523	1045.93
17A	5.0E-5	4.3532	1.41	.0201	.0094	188.31
17B		4.3532	1.22	.0209	.0085	169.42
18A		1.8234	1.73	.0731	.0420	840.29
18B		1.8234	1.41	.0731	.0342	684.86
19A		3.7421	1.64	.1448	.0789	1051.92
19B		3.7421	1.50	.1315	.0655	873.75
20A	7.5E-5	4.3345	1.67	.0679	.0377	502.29
20B		4.3345	1.54	.0662	.0339	451.60



# Hofstee Plot Parameters

Sample Number	Concentration (Molar NH4)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basis
21A		5.6959	1.84	.0935	.0572	762.08
21B		5.6959	1.48	.0968	.0476	634.61
22A		4.0259	1.47	.1080	.0527	527.44
22B		4.0259	1.55	.1237	.0637	636.99
23A	1.0E-4	9.6917	1.54	.0764	.0391	390.88
23B		9.6917	1.36	.0673	.0304	304.08
24A		7.1317	2.08	.0909	.0628	628.15
24B		7.1317	1.84	.0975	.0596	596.01
25A		6.3985	1.66	.1749	.0965	385.83
25B		6.3985	1.36	.1763	.0797	318.63
26A	2.5E-4	4.2761	1.97	.0786	.0514	205.77
26B		4.2761	2.10	.0792	.0553	221.02
27A		7.6330	1.75	.1631	.0948	379.30
27B		7.6330	1.57	.1697	.0885	354.06
28A		3.8035	1.52	.1411	.0713	142.51
28B		3.8035	1.61	.1423	.0761	152.23
29A	5.0E-4	2.7176	1.95	.1014	.0657	131.38
29B		2.7176	1.69	.1017	.0571	114.20
30A		4.2963	1.01	.1526	.0512	102.41
30B		4.2963	1.22	.1517	.0615	122.97
31A		3.8698	1.82	.1499	.0906	120.85
31B		3.8698	1.39	.1474	.0681	90.76
32A	7.5E-4	3.8616	1.59	.1094	.0578	77.05
32B		3.8616	1.66	.1101	.0607	80.96
33A		3.6805	1.68	.2394	.1336	178.16
33B		3.6805	1.54	.2411	.1234	164.47
34A		2.5354	1.68	.1818	.1015	101.47
34B		2.5354	1.58	.1948	.1023	102.25
35A	1.0E-3	5.0345	1.68	.1987	.1109	110.90
35B		5.0345	1.27	.2230	.0941	94.09
36A		7.3960	1.13	.1393	.0523	52.30
36B		7.3960	1.23	.1690	.0691	69.06
37A		3.5097	2.13	.1474	.1043	41.72
37B		3.5097	1.84	.1512	.0924	36.97
38A	2.5E-3	4.4880	1.38	.2701	.1238	49.53
38B		4.4880	1.21	.2551	.1025	41.02
39A		2.9159	1.18	.2125	.0833	33.32
39B		2.9159	1.08	.2128	.0764	30.54
40A		2.4256	2.09	.2848	.1978	39.55
40B		2.4256	2.35	.3129	.2443	48.86
41A	5.0E-3	4.9891	1.27	.4108	.1733	34.67
41B		4.9891	1.17	.3531	.1373	27.45
42A		3.4647	1.35	.3450	.1547	30.95
42B		3.4647	1.16	.3049	.1175	23.50



Table D-8. Ammonium Uptake Kinetic Data for Columbia Needlegrass After 87 Days (30.0% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1		3.0779	1.66	.0111	.0061	2456.80
2	2.5E-6	4.6675	1.74	.0410	.0238	9512.00
3		2.6712	1.72	.0088	.0050	2018.13
4		3.3177	1.49	.0129	.0064	1281.40
5	5.0E-6	3.7333	1.61	.0131	.0070	1406.07
6		5.1014	1.58	.0054	.0028	568.80
7		4.6834	1.58	.0104	.0055	730.31
8	7.5E-6	5.4802	1.69	.0068	.0038	510.76
9		3.0658	1.73	.0098	.0057	753.51
10		4.7952	1.67	.0132	.0073	734.80
11	1.0E-5	4.5673	1.63	.0115	.0062	624.83
12		5.0130	1.87	.0098	.0061	610.87
13		4.0967	1.72	.0183	.0105	419.68
14	2.5E-5	3.1023	1.78	.0168	.0100	398.72
15		2.5229	1.72	.0258	.0148	591.68
16		6.6717	1.66	.0265	.0147	293.27
17	5.0E-5	5.0914	1.64	.0265	.0145	289.73
18		5.8928	1.57	.0294	.0154	307.72
19		3.4993	1.68	.0401	.0225	299.41
20	7.5E-5	2.6147	1.95	.0273	.0177	236.60
21		5.3978	1.69	.0252	.0142	189.28
22		3.2368	1.51	.0501	.0252	252.17
23	1.0E-4	3.7377	1.63	.0588	.0319	319.48
24		3.9372	1.71	.0465	.0265	265.05
25		5.6842	1.68	.0867	.0486	194.21
26	2.5E-4	8.1539	1.56	.0635	.0330	132.08
27		2.5423	1.63	.0720	.0391	156.48
28		4.3764	1.61	.1173	.0630	125.90
29	5.0E-4	3.8861	1.56	.1169	.0608	121.58
30		4.0119	1.67	.1158	.0645	128.92
31		4.9310	1.56	.0965	.0502	66.91
32	7.5E-4	3.8183	1.74	.0928	.0538	71.77
33		2.6430	1.67	.1149	.0640	85.28
34		5.6417	1.49	.0857	.0426	42.56
35	1.0E-3	3.3300	1.63	.1150	.0625	62.48
36		7.2144	1.69	.1529	.0861	86.13
37		3.6005	1.58	.1767	.0931	37.22
38	2.5E-3	2.7065	1.83	.1676	.1022	40.89
39		2.5206	1.59	.1259	.0667	26.69
40		4.8222	1.72	.1436	.0823	16.47
41	5.0E-3	5.3498	1.62	.2536	.1369	27.39
42		2.5188	1.78	.0861	.0511	10.22



Table D-9. Ammonium Uptake Kinetic Data for Slender Wheatgrass After 15 Days (31.0% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1		.0763	3.34	.0628	.0677	27064.77
2	2.5E-6	.0757	2.89	.0589	.0549	21964.00
3		.0664	2.64	.1244	.1059	42376.26
4		.0746	3.00	.1115	.1079	21580.65
5	5.0E-6	.0617	3.15	.1331	.1352	27049.35
6		.0781	3.25	.1433	.1502	30046.77
7		.0944	3.21	.1563	.1618	21579.48
8	7.5E-6	.0575	2.85	.1152	.1059	14121.29
9		.0493	2.95	.1340	.1275	17002.15
10		.0537	3.45	.2176	.2422	24216.77
11	1.0E-5	.0720	2.88	.1855	.1723	17233.55
12		.0809	2.80	.1982	.1790	17901.94
13		.0647	3.59	.2341	.2711	10844.12
14	2.5E-5	.0685	2.78	.3189	.2860	11439.25
15		.0723	2.73	.3759	.3310	13241.38
16		.0770	3.29	.3854	.4090	8180.43
17	5.0E-5	.0662	2.82	.3589	.3265	6529.66
18		.0733	3.61	.2994	.3487	6973.12
19		.0511	3.01	.4354	.4228	5636.79
20	7.5E-5	.0592	3.61	.3061	.3565	4752.78
21		.0585	4.04	.2928	.3816	5087.79
22		.0610	2.81	.4490	.4070	4069.97
23	1.0E-4	.0729	3.20	.4450	.4594	4593.55
24		.0633	2.90	.4256	.3981	3981.42
25		.0588	3.26	.4729	.4973	1989.23
26	2.5E-4	.0650	2.96	.5611	.5358	2143.04
27		.0569	3.19	.4566	.4699	1879.42
28		.0807	3.44	.5619	.6235	1247.06
29	5.0E-4	.0755	4.08	.4063	.5347	1069.49
30		.0693	3.18	.5762	.5911	1182.14
31		.0777	3.87	.3431	.4283	571.10
32	7.5E-4	.0614	3.59	.5805	.6723	896.34
33		.0573	3.03	.7229	.7066	942.10
34		.0731	3.00	.7141	.6911	691.06
35	1.0E-3	.1092	3.22	.6434	.6683	668.31
36		.0639	3.80	.5832	.7149	714.89
37		.0725	2.87	.8684	.8040	321.59
38	2.5E-3	.0683	4.00	.4662	.6015	240.62
39		.0362	2.94	.8732	.8281	331.25
40		.0475	3.15	.9815	.9973	199.47
41	5.0E-3	.0611	3.67	.6718	.7953	159.06
42		.0741	2.97	.8202	.7858	157.16





Table D-10. Ammonium Uptake Kinetic Data for Slender Wheatgrass After 58 Days (31.6% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1		2.1240	1.34	.0646	.0274	10957.47
2	2.5E-6	2.3010	1.45	.0405	.0186	7433.54
3		2.7640	1.44	.0678	.0309	12358.48
4		3.2854	1.45	.0400	.0184	3670.89
5	5.0E-6	2.2305	1.60	.0334	.0169	3382.28
6		2.9603	1.41	.0289	.0129	2579.05
7		2.4915	1.76	.0354	.0197	2628.86
8	7.5E-6	2.2471	1.52	.0475	.0228	3046.41
9		2.4128	1.31	.0524	.0217	2896.37
10		2.1998	1.37	.0563	.0244	2440.85
11	1.0E-5	2.4121	1.58	.0529	.0264	2645.00
12		2.0564	1.23	.0407	.0158	1584.21
13		2.4022	1.74	.0674	.0371	1484.51
14	2.5E-5	2.0239	1.74	.1147	.0632	2526.30
15		1.7204	1.45	.1232	.0565	2261.27
16		1.9949	1.59	.1045	.0526	1051.61
17	5.0E-5	3.1392	1.52	.1205	.0580	1159.24
18		1.7580	1.40	.1555	.0689	1377.85
19		2.2159	1.52	.1347	.0648	863.90
20	7.5E-5	2.2001	1.75	.1345	.0745	993.14
21		2.5979	1.28	.1365	.0553	737.22
22		2.1195	1.31	.1652	.0685	684.85
23	1.0E-4	2.1327	1.27	.1360	.0547	546.58
24		2.0188	1.49	.1227	.0579	578.55
25		2.4027	1.61	.1898	.0967	386.81
26	2.5E-4	3.2666	1.96	.5355	.3321	1328.58
27		2.3851	2.36	.5279	.3943	1577.02
28		2.5077	1.28	.4481	.1815	363.02
29	5.0E-4	2.3541	1.21	.4312	.1651	330.22
30		2.5389	1.32	.3831	.1600	320.06
31		2.2538	1.66	.4172	.2192	292.22
32	7.5E-4	2.5169	1.42	.2685	.1207	160.87
33		1.7094	1.69	.2680	.1433	191.11
34		2.3789	1.50	.3215	.1526	152.61
35	1.0E-3	2.5558	1.51	.3415	.1632	163.19
36		2.0762	1.59	.3235	.1628	162.77
37		2.1046	1.46	.3125	.1444	57.75
38	2.5E-3	2.4385	1.32	.5124	.2140	85.62
39		2.2560	1.68	.3071	.1633	65.31
40		2.1698	1.34	.5211	.2210	44.19
41	5.0E-3	2.1866	1.52	.4083	.1964	39.28
42		1.8194	1.79	.4057	.2298	45.96



Table D-11. Ammonium Uptake Kinetic Data for Slender Wheatgrass After 78 Days (30.1% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis	
1A		11.8423	1.93	.0083	.0053	2128.77	
1B		11.8423	2.05	.0080	.0054	2179.40	
2A	2.5E-6	10.5401	2.02	.0112	.0075	3006.51	
2B		10.5401	1.92	.0110	.0070	2806.64	
3A		8.9027	2.14	.0124	.0088	3526.38	
3B		8.9027	2.15	.0123	.0088	3514.29	
4A		9.2828	2.02	.0110	.0074	1476.41	
4B		9.2828	2.13	.0112	.0079	1585.12	
5A	5.0E-6	8.5874	2.38	.0078	.0062	1233.49	
5B		8.5874	2.20	.0083	.0061	1213.29	
6A		11.4422	2.01	.0098	.0065	1308.84	
6B		11.4422	1.97	.0107	.0070	1400.60	
7A		9.3461	2.41	.0117	.0094	1249.04	
7B		9.3461	2.29	.0130	.0099	1318.72	
8A	7.5E-6	10.7698	2.02	.0147	.0099	1315.35	
8B		10.7698	2.00	.0149	.0099	1320.04	
9A		3.7820	1.71	.0157	.0089	1189.24	
9B		3.7820	1.78	.0145	.0086	1143.30	
10A		11.0875	1.86	.0128	.0079	790.96	
10B		11.0875	1.83	.0129	.0078	784.29	
11A	1.0E-5	7.1112	2.21	.0164	.0120	1204.12	
11B		7.1112	2.06	.0182	.0125	1245.58	
12A		3.5885	2.09	.0131	.0091	909.60	
12B		3.5885	2.28	.0129	.0098	977.14	
13A		9.2854	1.75	.0224	.0130	520.93	
13B		9.2854	1.90	.0212	.0134	535.28	
14A	2.5E-5	10.0058	1.56	.0243	.0126	503.76	
14B		10.0058	1.87	.0212	.0132	526.83	
15A		5.0191	2.12	.0166	.0117	467.67	
15B		5.0191	2.07	.0187	.0129	514.41	
16A		9.8261	1.78	.0341	.0202	403.31	
16B		9.8261	1.80	.0304	.0182	363.59	
17A	5.0E-5	7.7869	2.09	.0294	.0204	408.28	
17B		7.7869	2.07	.0313	.0215	430.50	
18A		8.0242	2.11	.0239	.0168	335.08	
18B		8.0242	2.21	.0207	.0152	303.97	
19A		8.0810	2.71	.0254	.0229	304.91	
19B		8.0810	2.76	.0258	.0237	315.43	
20A	7.5E-5	9.8339	1.94	.0300	.0193	257.81	
20B		9.8339	2.08	.0242	.0167	222.97	



## Hofstee Plot Parameters

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
21A		11.8714	1.78	.0327	.0193	257.83
21B		11.8714	1.81	.0358	.0215	287.03
22A		7.9851	2.10	.0416	.0290	290.23
22B		7.9851	2.14	.0413	.0294	293.63
23A	1.0E-4	11.0269	2.10	.0301	.0210	210.00
23B		11.0269	2.11	.0319	.0224	223.62
24A		11.7191	2.00	.0330	.0219	219.27
24B		11.7191	2.29	.0299	.0227	227.48
25A		7.9317	2.10	.0468	.0327	130.60
25B		7.9317	2.06	.0430	.0294	117.71
26A	2.5E-4	10.4377	1.83	.0432	.0263	105.06
26B		10.4377	1.94	.0399	.0257	102.87
27A		7.1961	2.18	.0295	.0214	85.46
27B		7.1961	2.15	.0312	.0223	89.14
28A		7.5348	2.12	.0271	.0191	38.17
28B		7.5348	2.04	.0371	.0251	50.29
29A	5.0E-4	12.1357	1.96	.0567	.0369	73.84
29B		12.1357	2.13	.0533	.0377	75.43
30A		7.5853	2.37	.0487	.0383	76.69
30B		7.5853	2.34	.0502	.0390	78.05
31A		6.9895	2.04	.0676	.0458	61.09
31B		6.9895	2.33	.0682	.0528	70.39
32A	7.5E-4	10.1793	2.26	.0422	.0317	42.25
32B		10.1793	2.34	.0429	.0334	44.47
33A		9.4039	2.05	.0477	.0325	43.32
33B		9.4039	2.23	.0506	.0375	49.98
34A		7.2927	1.95	.0474	.0307	30.71
34B		7.2927	2.04	.0470	.0319	31.85
35A	1.0E-3	8.0497	2.15	.0486	.0347	34.71
35B		8.0497	2.22	.0472	.0348	34.81
36A		10.3964	1.88	.0771	.0482	48.16
36B		10.3964	2.07	.0691	.0475	47.52
37A		8.1397	2.20	.0712	.0520	20.82
37B		8.1397	2.21	.0704	.0517	20.68
38A	2.5E-3	6.1975	2.33	.0657	.0509	20.34
38B		6.1975	2.32	.0620	.0478	19.11
39A		10.1279	1.91	.0660	.0419	16.75
39B		10.1279	1.91	.0626	.0397	15.89
40A		9.3052	1.96	.0886	.0577	11.54
40B		9.3052	1.82	.0905	.0547	10.94
41A	5.0E-3	9.7848	2.07	.1142	.0785	15.71
41B		9.7848	2.07	.0986	.0678	13.56
42A		11.6937	2.01	.0956	.0638	12.77
42B		11.6937	2.03	.1001	.0675	13.50



Table D-12. Ammonium Uptake Kinetic Data for Magna Smooth Brome After 15 Days (31.0% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis	
1		.0832	2.74	.0570	.0504	20152.26	
2	2.5E-6	.0971	1.94	.0759	.0475	18999.48	
3		.1624	1.64	.0719	.0380	15214.97	
4		.1075	2.42	.1197	.0934	18688.65	
5	5.0E-6	.1047	1.95	.1225	.0771	15411.29	
6		.1061	2.44	.0893	.0703	14057.55	
7		.1163	2.07	.1767	.1180	15732.00	
8	7.5E-6	.0635	2.29	.1578	.1166	15542.45	
9		.1089	2.24	.1226	.0886	11811.78	
10		.0891	2.69	.1492	.1295	12946.71	
11	1.0E-5	.0928	1.92	.2073	.1284	12839.23	
12		.1085	2.62	.1727	.1460	14595.94	
13		.0748	1.85	.3695	.2205	8820.32	
14	2.5E-5	.1130	2.22	.3549	.2542	10166.17	
15		.0893	2.21	.3066	.2186	8743.05	
16		.0860	2.38	.4574	.3512	7023.30	
17	5.0E-5	.1136	2.48	.3496	.2797	5593.60	
18		.1131	2.50	.3811	.3073	6146.77	
19		.0668	2.39	.3979	.3068	4090.24	
20	7.5E-5	.1077	2.64	.4274	.3640	4853.06	
21		.1184	2.20	.4201	.2981	3975.14	
22		.0689	2.42	.4625	.3610	3610.48	
23	1.0E-4	.0955	2.67	.4597	.3959	3959.35	
24		.0867	2.29	.5191	.3835	3834.64	
25		.0831	2.16	.6555	.4567	1826.94	
26	2.5E-4	.0575	2.95	.5202	.4950	1980.12	
27		.0909	2.02	.7336	.4780	1912.09	
28		.0645	2.19	.8644	.6107	1221.31	
29	5.0E-4	.0742	2.38	.6172	.4739	947.70	
30		.0840	2.12	.8534	.5836	1167.23	
31		.0517	2.27	.9942	.7280	970.68	
32	7.5E-4	.1104	2.23	.7101	.5108	681.09	
33		.0729	2.04	.8295	.5459	727.82	
34		.0300	2.57	.8603	.7132	713.22	
35	1.0E-3	.0984	2.72	.6774	.5944	594.36	
36		.1322	1.86	.6846	.4108	410.76	
37		.0309	2.36	1.1238	.8555	342.22	
38	2.5E-3	.0674	2.66	1.0394	.8919	356.75	
39		.0794	1.96	1.0417	.6586	263.45	
40		.0452	2.29	1.5855	1.1712	234.24	
41	5.0E-3	.0831	1.95	1.0799	.6793	135.86	
42		.0589	2.04	1.3323	.8767	175.35	





Table D-13. Ammonium Uptake Kinetic Data for Magna Smooth Brome After 39 Days (32.2% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1		.9241	.41	.1521	.0194	7746.71
2	2.5E-6	.4383	1.22	.0628	.0238	9517.52
3		.5459	.73	.1975	.0448	17909.94
4		.4684	.96	.0002	.0001	11.93
5	5.0E-6	.6919	.84	.0572	.0149	2984.35
6		.2602	1.12	.0413	.0144	2873.04
7		.7209	1.09	.1646	.0557	7429.15
8	7.5E-6	.6198	1.03	.0537	.0172	2290.31
9		.5300	.97	.5225	.1574	20986.54
10		.3418	.97	.0474	.0143	1427.89
11	1.0E-5	.4585	1.16	.0615	.0222	2215.53
12		.6473	1.15	.0764	.0273	2728.57
13		.6492	1.00	.0000	.0000	.00
14	2.5E-5	.5681	1.09	.7570	.2563	10250.06
15		.5106	1.07	.0769	.0256	1022.15
16		.3171	1.00	.0000	.0000	.00
17	5.0E-5	.4819	1.23	.1460	.0558	1115.40
18		.5196	1.15	.1395	.0498	996.43
19		.6132	1.23	.1253	.0479	638.17
20	7.5E-5	.5888	1.10	.0037	.0013	16.85
21		.5471	1.35	.0383	.0161	214.10
22		.4469	1.07	.2443	.0812	811.80
23	1.0E-4	.6280	1.07	.3497	.1162	1162.05
24		.3500	1.26	.2797	.1094	1094.48
25		.4863	1.46	.4801	.2177	870.74
26	2.5E-4	.4950	1.08	.7404	.2483	993.33
27		.5165	1.61	.1780	.0890	356.00
28		.3961	1.29	.0212	.0085	16.99
29	5.0E-4	.3739	1.36	.2899	.1224	244.88
30		.5438	1.19	.8276	.3059	611.70
31		.6075	1.65	.2479	.1270	169.37
32	7.5E-4	.4522	1.52	.3602	.1700	226.71
33		.6705	.96	.5027	.1499	199.83
34		.3786	1.16	.1655	.0596	59.62
35	1.0E-3	.4225	1.34	.1928	.0802	80.23
36		.4269	1.00	.0000	.0000	.00
37		.5110	1.24	.6522	.2512	100.46
38	2.5E-3	.5985	1.00	.7724	.2399	95.95
39		.2873	1.48	.2007	.0922	36.90
40		.6252	1.00	.0000	.0000	.00
41	5.0E-3	.5285	1.36	.2910	.1229	24.58
42		.4592	1.00	.0000	.0000	.00



Table D-14. Ammonium Uptake Kinetic Data for Magna Smooth Brome After 78 Days (30.3% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1A		9.0223	1.82	1.8205	1.0939	437541.54
1B		9.0223	1.74	1.7417	1.0011	400449.15
2A	2.5E-6	13.2197	1.71	1.7103	.9654	386150.34
2B		13.2197	1.75	1.7542	1.0155	406216.96
3A		25.3842	1.48	1.4786	.7215	288614.26
3B		25.3842	1.52	1.5183	.7608	304313.40
4A	.	17.9087	1.29	1.2944	.5530	110595.83
4B		17.9087	1.32	1.3226	.5773	115459.52
5A	5.0E-6	16.1865	1.63	1.6290	.8758	175168.05
5B		16.1865	1.62	1.6155	.8613	172264.72
6A		6.3001	1.58	1.5832	.8273	165453.24
6B		6.3001	1.70	1.6990	.9527	190543.91
7A		13.4156	1.55	1.5462	.7890	105206.58
7B		13.4156	1.62	1.6157	.8615	114866.09
8A	7.5E-6	8.0336	1.65	1.6466	.8948	119303.53
8B		8.0336	1.97	1.9661	1.2758	170105.59
9A		13.3483	1.44	1.4396	.6840	91195.55
9B		13.3483	1.77	1.7707	1.0348	137975.58
10A		25.3858	1.18	1.1796	.4592	45920.48
10B		25.3858	1.24	1.2418	.5089	50893.47
11A	1.0E-5	7.2532	1.46	1.4614	.7049	70488.14
11B		7.2532	1.41	1.4108	.6569	65686.83
12A		15.2869	1.53	1.5302	.7728	77280.58
12B		15.2869	1.67	1.6698	.9202	92018.49
13A		19.2302	1.55	1.5487	.7916	31664.08
13B		19.2302	1.60	1.6024	.8474	33897.67
14A	2.5E-5	14.7773	1.48	1.4768	.7198	28790.75
14B		14.7773	1.51	1.5139	.7564	30255.36
15A		16.3791	1.70	1.6958	.9490	37961.77
15B		16.3791	1.89	1.8872	1.1754	47017.71
16A		8.2280	2.11	2.1060	1.4638	29275.05
16B		8.2280	2.15	2.1464	1.5204	30408.57
17A	5.0E-5	18.1752	1.68	1.6756	.9266	18531.42
17B		18.1752	1.89	1.8864	1.1744	23487.36
18A		18.0736	1.25	1.2508	.5163	10326.17
18B		18.0736	1.49	1.4875	.7302	14604.77
19A		14.9302	1.64	1.6440	.8920	11892.98
19B		14.9302	1.54	1.5388	.7815	10420.27
20A	7.5E-5	14.6946	1.94	1.9402	1.2424	16565.43
20B		14.6946	1.73	1.7283	.9858	13143.64



## Hofstee Plot Parameters

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
21A		11.5203	1.67	1.6709	.9214	12285.97
21B		11.5203	1.63	1.6290	.8757	11676.58
22A		22.2250	1.53	1.5288	.7714	7713.95
22B		22.2250	1.44	1.4439	.6881	6880.83
23A	1.0E-4	12.9012	2.07	2.0727	1.4178	14177.88
23B		12.9012	2.03	2.0317	1.3623	13622.53
24A		21.0964	1.51	1.5077	.7502	7501.79
24B		21.0964	1.45	1.4524	.6962	6962.16
25A		18.9915	1.51	1.5071	.7497	2998.62
25B		18.9915	1.66	1.6611	.9106	3642.43
26A	2.5E-4	15.7846	1.47	1.4699	.7130	2852.14
26B		15.7846	1.55	1.5537	.7967	3186.84
27A		16.5224	1.41	1.4108	.6568	2627.37
27B		16.5224	1.36	1.3622	.6124	2449.70
28A		8.3758	1.86	1.8590	1.1406	2281.16
28B		8.3758	1.88	1.8797	1.1661	2332.24
29A	5.0E-4	10.1994	1.50	1.5036	.7461	1492.23
29B		10.1994	1.57	1.5703	.8138	1627.65
30A		11.8816	1.57	1.5743	.8179	1635.88
30B		11.8816	1.46	1.4552	.6988	1397.68
31A		11.4067	2.05	2.0488	1.3853	1847.05
31B		11.4067	2.01	2.0064	1.3286	1771.42
32A	7.5E-4	6.1510	2.00	2.0007	1.3211	1761.44
32B		6.1510	2.03	2.0334	1.3646	1819.53
33A		12.1688	1.53	1.5287	.7712	1028.29
33B		12.1688	1.71	1.7072	.9619	1282.59
34A		6.5989	2.01	2.0052	1.3271	1327.07
34B		6.5989	1.96	1.9609	1.2691	1269.08
35A	1.0E-3	9.1673	1.87	1.8749	1.1602	1160.20
35B		9.1673	1.90	1.8957	1.1860	1186.00
36A		14.8557	1.63	1.6311	.8780	878.00
36B		14.8557	1.49	1.4896	.7324	732.36
37A		9.0326	2.14	2.1361	1.5060	602.39
37B		9.0326	2.04	2.0379	1.3706	548.25
38A	2.5E-3	9.9722	1.88	1.8788	1.1650	465.99
38B		9.9722	1.86	1.8566	1.1376	455.05
39A		12.1776	1.37	1.3695	.6189	247.58
39B		12.1776	1.37	1.3718	.6210	248.41
40A		22.9503	1.39	1.3923	.6398	127.96
40B		22.9503	1.50	1.4989	.7415	148.30
41A	5.0E-3	25.9279	1.57	1.5665	.8099	161.97
41B		25.9279	1.47	1.4658	.7091	141.83
42A		13.9986	1.57	1.5709	.8144	162.88
42B		13.9986	1.21	1.2092	.4826	96.51



Table D-15. Ammonium Uptake Kinetic Data for Magna Smooth Brome After 87 Days (30.0% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis	
1		4.1885	1.48	.0131	.0065	2585.07	
2	2.5E-6	4.5617	1.78	.0080	.0047	1898.67	
3		2.7723	2.36	.0131	.0103	4122.13	
4		4.4458	1.33	.0139	.0062	1232.47	
5	5.0E-6	3.8482	2.34	.0099	.0077	1544.40	
6		6.7009	1.53	.0095	.0048	969.00	
7		3.5604	2.05	.0123	.0084	1120.67	
8	7.5E-6	5.8636	1.65	.0082	.0045	601.33	
9		7.6608	1.45	.0099	.0048	638.00	
10		4.6246	1.64	.0138	.0075	754.40	
11	1.0E-5	7.1305	1.57	.0132	.0069	690.80	
12		6.0080	1.67	.0105	.0058	584.50	
13		4.0426	1.68	.0314	.0176	703.36	
14	2.5E-5	10.2948	1.49	.0197	.0098	391.37	
15		8.7426	1.63	.0117	.0064	254.28	
16		4.5559	1.96	.0386	.0252	504.37	
17	5.0E-5	4.1121	1.59	.0513	.0272	543.78	
18		4.8013	2.07	.0327	.0226	451.26	
19		6.4758	1.68	.0388	.0217	289.71	
20	7.5E-5	4.0994	1.54	.0428	.0220	292.94	
21		9.4206	.82	.0348	.0095	126.83	
22		7.8861	.98	.0415	.0136	135.57	
23	1.0E-4	3.8912	1.54	.0420	.0216	215.60	
24		2.5916	2.06	.0475	.0326	326.17	
25		8.0534	1.53	.0668	.0341	136.27	
26	2.5E-4	8.4378	1.87	.0608	.0379	151.59	
27		4.3189	2.08	.0381	.0264	105.66	
28		4.1227	1.78	.1053	.0625	124.96	
29	5.0E-4	3.2751	2.04	.0923	.0628	125.53	
30		5.2493	1.86	.1104	.0684	136.90	
31		8.2678	1.80	.1074	.0644	85.92	
32	7.5E-4	8.0729	1.88	.0749	.0469	62.58	
33		5.8620	1.74	.0571	.0331	44.16	
34		4.0289	1.63	.0902	.0490	49.01	
35	1.0E-3	4.2184	1.89	.0489	.0308	30.81	
36		8.7221	1.65	.0628	.0345	34.54	
37		7.5937	1.59	.0982	.0520	20.82	
38	2.5E-3	4.6461	2.13	.0924	.0656	26.24	
39		6.7662	1.81	.1867	.1126	45.06	
40		7.4196	1.56	.2014	.1047	20.95	
41	5.0E-3	7.1165	1.67	.1189	.0662	13.24	
42		5.8159	1.72	.1506	.0863	17.27	





E. Nitrate Uptake Kinetic Data for Experiments Using Nitrate  
Plus Nutrient Solution



Table E-1. Nitrate Uptake Kinetic Data for Alpine Sheep Fescue After 16 Days (35.3% Excess 15N)

Sample Number	Concentration (Molar NO <sub>3</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis	
1		.0257	3.83	.0710	.0770	15406.80	
2	5.0E-6	.0156	4.13	.0789	.0923	18462.15	
3		.0178	4.21	.0693	.0826	16529.92	
4		.0291	3.80	.1259	.1355	18070.63	
5	7.5E-6	.0205	4.27	.1228	.1485	19805.70	
6		.0212	3.70	.0964	.1010	13472.33	
7		.0404	3.41	.1098	.1061	10606.74	
8	1.0E-5	.0146	4.36	.1333	.1646	16464.25	
9		.0146	4.39	.1055	.1312	13120.25	
10		.0376	4.00	.1473	.1669	6676.49	
11	2.5E-5	.0194	4.33	.1239	.1520	6079.17	
12		.0186	3.97	.0957	.1076	4305.14	
13		.0326	4.29	.1566	.1903	3806.31	
14	5.0E-5	.0165	3.97	.1156	.1300	2600.18	
15		.0208	3.75	.1430	.1519	3038.24	
16		.0391	3.74	.1488	.1577	2102.03	
17	7.5E-5	.0148	3.90	.1939	.2142	2856.32	
18		.0232	4.20	.1296	.1542	2055.98	
19		.0413	4.01	.1356	.1540	1540.39	
20	1.0E-4	.0176	3.91	.1908	.2113	2113.39	
21		.0273	3.77	.1198	.1279	1279.45	
22		.0276	4.06	.1343	.1545	617.86	
23	2.5E-4	.0173	4.14	.1740	.2041	816.27	
24		.0243	4.19	.1828	.2170	867.91	
25		.0347	4.33	.1744	.2139	427.85	
26	5.0E-4	.0118	4.13	.2086	.2441	488.11	
27		.0206	4.51	.1835	.2344	468.89	
28		.0333	4.20	.1963	.2336	311.41	
29	7.5E-4	.0147	4.11	.1988	.2315	308.62	
30		.0244	4.22	.2358	.2819	375.85	
31		.0278	4.03	.1720	.1964	196.36	
32	1.0E-3	.0209	3.70	.2283	.2393	239.29	
33		.0257	4.01	.1703	.1935	193.46	
34		.0294	4.11	.2471	.2877	115.08	
35	2.5E-3	.0169	4.18	.2577	.3052	122.06	
36		.0229	4.03	.1987	.2268	90.74	
37		.0238	3.79	.3068	.3294	65.88	
38	5.0E-3	.0180	4.26	.2723	.3286	65.72	
39		.0235	3.74	.3217	.3408	68.17	
40		.0305	3.80	.3196	.3440	34.40	
41	1.0E-2	.0304	3.94	.3159	.3526	35.26	
42		.0251	3.99	.3580	.4047	40.47	



Table E-2. Nitrate Uptake Kinetic Data for Alpine Sheep Fescue After 79 Days (35.3 % Excess 15N)

Sample Number	Concentration (Molar NO <sub>3</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basls
1A		1.0796	1.26	.0929	.0332	6631.95
1B		1.0796	1.08	.0635	.0194	3885.55
2A	5.0E-6	1.3767	1.69	.0449	.0215	4299.21
2B		1.3767	1.60	.0473	.0214	4287.82
3A		1.3331	1.62	.0554	.0254	5084.87
3B		1.3331	1.50	.0512	.0218	4351.27
4A		1.7038	.94	.0566	.0151	2009.59
4B		1.7038	.99	.0653	.0183	2441.81
5A	7.5E-6	2.0474	1.58	.0488	.0218	2912.33
5B		2.0474	1.61	.0448	.0204	2724.38
6A		1.6640	1.83	.0636	.0330	4396.15
6B		1.6640	2.14	.0584	.0354	4720.53
7A		1.7897	1.29	.0555	.0203	2028.19
7B		1.7897	1.45	.0568	.0233	2333.14
8A	1.0E-5	1.5906	1.01	.0727	.0208	2080.08
8B		1.5906	1.65	.0577	.0270	2697.03
9A		.8053	1.69	.0481	.0230	2302.80
9B		.8053	2.26	.0319	.0204	2042.32
10A		1.9511	1.08	.1107	.0339	1354.74
10B		1.9511	1.59	.0815	.0367	1468.39
11A	2.5E-5	1.3934	2.26	.0463	.0296	1185.70
11B		1.3934	2.04	.0457	.0264	1056.41
12A		1.4870	1.64	.1011	.0470	1878.80
12B		1.4870	1.86	.0778	.0410	1639.75
13A		2.2002	1.48	.1272	.0533	1066.61
13B		2.2002	1.51	.1105	.0473	945.35
14A	5.0E-5	1.2339	1.87	.1016	.0538	1076.44
14B		1.2339	2.18	.0832	.0514	1027.63
15A		1.3146	1.79	.1299	.0659	1317.40
15B		1.3146	2.38	.0903	.0609	1217.64
16A		.9453	1.64	.0799	.0371	494.94
16B		.9453	2.25	.0671	.0428	570.25
17A	7.5E-5	1.6119	1.94	.1153	.0634	844.88
17B		1.6119	1.77	.1129	.0566	754.80
18A		2.1297	1.64	.1004	.0466	621.93
18B		2.1297	1.78	.0908	.0458	610.48
19A		1.7841	1.08	.1153	.0353	352.76
19B		1.7841	1.16	.1197	.0393	393.35
20A	1.0E-4	1.1766	2.11	.0753	.0450	450.09
20B		1.1766	2.40	.0522	.0355	354.90



Sample Number	Concen- tration (Molar N03)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basis
21A		1.7029	1.46	.0843	.0349	348.66
21B		1.7029	1.87	.0856	.0453	453.46
22A		1.2981	1.78	.1168	.0589	235.59
22B		1.2981	1.73	.1188	.0582	232.89
23A	2.5E-4	1.6499	2.34	.1210	.0802	320.84
23B		1.6499	2.48	.1047	.0736	294.23
24A		1.5143	1.72	.1456	.0709	283.78
24B		1.5143	1.90	.1332	.0717	286.78
25A		1.0176	1.78	.1341	.0676	135.24
25B		1.0176	2.18	.1260	.0778	155.63
26A	5.0E-4	1.4864	1.89	.1396	.0747	149.49
26B		1.4864	2.38	.0992	.0669	133.77
27A		1.1293	1.98	.1337	.0750	149.99
27B		1.1293	1.31	.1542	.0572	114.45
28A		1.0212	1.34	.1537	.0583	77.79
28B		1.0212	1.98	.1661	.0932	124.22
29A	7.5E-4	1.0734	1.27	.1584	.0570	75.98
29B		1.0734	2.10	.1340	.0797	106.29
30A		1.3426	1.69	.1034	.0495	66.00
30B		1.3426	1.93	.0985	.0539	71.81
31A		2.3052	1.59	.1594	.0718	71.80
31B		2.3052	1.15	.1613	.0525	52.55
32A	1.0E-3	1.3028	1.20	.1654	.0562	56.23
32B		1.3028	1.80	.1680	.0857	85.67
33A		1.5775	1.42	.3738	.1504	150.37
33B		1.5775	2.09	.1272	.0753	75.31
34A		1.8812	1.28	.3069	.1113	44.51
34B		1.8812	1.09	.2176	.0672	26.88
35A	2.5E-3	1.9457	.68	.3603	.0694	27.76
35B		1.9457	.93	.2655	.0699	27.98
36A		1.1952	1.94	.2160	.1187	47.48
36B		1.1952	1.34	.2343	.0889	35.58
37A		1.5309	.70	.3271	.0649	12.97
37B		1.5309	1.23	.2980	.1038	20.77
38A	5.0E-3	1.7122	1.32	.3311	.1238	24.76
38B		1.7122	1.43	.3215	.1302	26.05
39A		1.1583	1.47	.2765	.1151	23.03
39B		1.1583	2.19	.2414	.1498	29.95
40A		1.1966	.93	.4194	.1105	11.05
40B		1.1966	1.91	.4063	.2198	21.98
41A	1.0E-3	.8279	1.96	.5159	.2864	28.64
41B		.8279	1.63	.5299	.2447	24.47
42A		1.2778	2.22	.3316	.2085	20.85
42B		1.2778	1.86	.3370	.1776	17.76





Table E-3. Nitrate Uptake Kinetic Data for Columbia Needlegrass After 15 Days (35.5% Excess 15N)

Sample Number	Concen- tration (Molar NO3)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis	
1		.0268	2.95	.1821	.1513	30264.51	
2	5.0E-6	.0231	2.48	.1521	.1063	21251.15	
3		.0241	2.72	.2783	.2132	42646.54	
4		.0233	2.64	.1249	.0929	12384.45	
5	7.5E-6	.0219	2.17	.1818	.1111	14817.13	
6		.0160	2.66	.1776	.1331	17743.32	
7		.0127	3.09	.1278	.1112	11124.00	
8	1.0E-5	.0246	2.50	.2609	.1837	18373.24	
9		.0228	2.89	.2089	.1701	17006.23	
10		.0349	1.77	.2362	.1178	4710.69	
11	2.5E-5	.0227	2.87	.1552	.1255	5018.86	
12		.0259	2.58	.2778	.2019	8075.76	
13		.0256	2.82	.2628	.2088	4175.19	
14	5.0E-5	.0163	2.21	.1935	.1205	2409.21	
15		.0232	2.59	.3076	.2244	4488.36	
16		.0215	2.88	.2354	.1910	2546.30	
17	7.5E-5	.0237	2.42	.3319	.2263	3016.71	
18		.0178	3.66	.1345	.1387	1848.90	
19		.0212	2.74	.1439	.1111	1110.66	
20	1.0E-4	.0212	2.61	.2578	.1895	1895.37	
21		.0222	3.12	.2881	.2532	2532.03	
22		.0344	3.04	.3280	.2809	1123.52	
23	2.5E-4	.0215	2.47	.3099	.2156	862.48	
24		.0286	2.47	.2744	.1909	763.68	
25		.0252	3.00	.2869	.2425	484.90	
26	5.0E-4	.0279	2.94	.3622	.3000	599.93	
27		.0295	2.44	.2353	.1617	323.45	
28		.0266	2.21	.3000	.1868	249.01	
29	7.5E-4	.0352	2.31	.3495	.2274	303.23	
30		.0244	2.52	.3545	.2516	335.53	
31		.0283	2.71	.3632	.2773	277.26	
32	1.0E-3	.0178	2.73	.3691	.2838	283.84	
33		.0159	3.04	.3082	.2639	263.92	
34		.0382	2.69	.4876	.3695	147.79	
35	2.5E-3	.0226	2.23	.3371	.2118	84.70	
36		.0204	2.73	.5709	.4390	175.61	
37		.0132	2.89	.3691	.3005	60.10	
38	5.0E-3	.0303	2.21	.5188	.3230	64.59	
39		.0367	2.03	.5568	.3184	63.68	
40		.0207	2.32	.7673	.5014	50.14	
41	1.0E-2	.0213	2.76	.7975	.6200	62.00	
42		.0207	2.86	.8290	.6679	66.79	



Table E-4. Nitrate Uptake Kinetic Data for Columbia Needlegrass After 84 Days (30.9% Excess 15N)

Sample Number	Concentration (Molar NO <sub>3</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basis	
1A		3.9513	2.12	.1239	.0850	17001.17	
1B		3.9513	1.99	.0742	.0478	9557.15	
2A	5.0E-6	3.1845	1.68	.0315	.0171	3425.24	
2B		3.1845	1.61	.0300	.0156	3126.21	
3A		3.0041	1.71	.0457	.0253	5058.06	
3B		3.0041	1.73	.0427	.0239	4781.29	
4A		2.5780	1.91	.0158	.0098	1302.18	
4B		2.5780	1.85	.0169	.0101	1349.08	
5A	7.5E-6	3.3611	1.92	.0204	.0127	1690.10	
5B		3.3611	2.00	.0205	.0133	1769.15	
6A		4.3536	1.85	.0501	.0300	3999.35	
6B		4.3536	1.64	.0272	.0144	1924.83	
7A		4.6176	1.80	.0199	.0116	1159.22	
7B		4.6176	1.66	.0219	.0118	1176.50	
8A	1.0E-5	1.7359	1.83	.0401	.0237	2374.85	
8B		1.7359	1.79	.0401	.0232	2322.94	
9A		2.4419	1.99	.0468	.0301	3013.98	
9B		2.4419	1.32	.0431	.0184	1841.17	
10A		1.5520	1.32	.0468	.0200	799.69	
10B		1.5520	1.91	.0326	.0202	806.03	
11A	2.5E-5	2.9158	1.75	.0439	.0249	994.50	
11B		2.9158	1.79	.0453	.0262	1049.67	
12A		2.2829	1.91	.0529	.0327	1307.95	
12B		2.2829	1.95	.0527	.0333	1330.29	
13A		6.2167	1.48	.0645	.0309	617.86	
13B		6.2167	1.20	.0666	.0259	517.28	
14A	5.0E-5	1.7125	2.05	.0623	.0413	826.63	
14B		1.7125	2.02	.0546	.0357	713.86	
15A		2.0034	1.96	.0696	.0441	882.95	
15B		2.0034	1.73	.0703	.0394	787.18	
16A		2.3361	1.81	.0403	.0236	314.75	
16B		2.3361	2.10	.0478	.0325	433.14	
17A	7.5E-5	2.9964	1.76	.0764	.0435	580.21	
17B		2.9964	1.82	.0714	.0421	560.72	
18A		1.8059	1.74	.0502	.0283	376.91	
18B		1.8059	1.83	.0492	.0291	388.50	
19A		2.0252	1.87	.0560	.0339	338.90	
19B		2.0252	1.86	.0499	.0300	300.37	
20A	1.0E-4	2.0431	2.37	.0531	.0407	407.27	
20B		2.0431	2.37	.0539	.0413	413.41	



## Hofstee Plot Parameters

Sample Number	Concentration (Molar NO3)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
21A		4.7974	1.59	.0780	.0401	401.36
21B		4.7974	1.46	.0868	.0410	410.12
22A		5.1105	1.94	.0766	.0481	192.37
22B		5.1105	1.41	.0800	.0365	146.02
23A	2.5E-4	1.5987	2.27	.0827	.0608	243.01
23B		1.5987	2.29	.0812	.0602	240.71
24A		6.6310	1.63	.1040	.0549	219.44
24B		6.6310	1.56	.1059	.0535	213.86
25A		4.1122	1.68	.1420	.0772	154.41
25B		4.1122	1.25	.1364	.0552	110.36
26A	5.0E-4	2.2582	2.21	.0950	.0679	135.89
26B		2.2582	2.06	.0966	.0644	128.80
27A		1.4489	2.03	.0796	.0523	104.59
27B		1.4489	1.79	.0755	.0437	87.47
28A		1.8192	1.76	.1029	.0586	78.15
28B		1.8192	1.86	.0964	.0580	77.37
29A	7.5E-4	2.1362	2.10	.1116	.0758	101.13
29B		2.1362	2.12	.1097	.0753	100.35
30A		3.1155	1.53	.1411	.0699	93.15
30B		3.1155	1.43	.1456	.0674	89.84
31A		4.1335	1.86	.1054	.0634	63.44
31B		4.1335	1.28	.1054	.0437	43.66
32A	1.0E-3	1.2338	2.16	.1450	.1014	101.36
32B		1.2338	2.26	.1347	.0985	98.52
33A		4.8915	1.47	.1725	.0821	82.06
33B		4.8915	2.09	.1746	.1181	118.10
34A		2.5092	2.10	.1863	.1266	50.64
34B		2.5092	2.05	.1818	.1206	48.24
35A	2.5E-3	2.9485	1.90	.1841	.1132	45.28
35B		2.9485	1.79	.1784	.1033	41.34
36A		5.6130	1.73	.1549	.0867	34.69
36B		5.6130	1.41	.1621	.0740	29.59
37A		3.6496	1.47	.2886	.1373	27.46
37B		3.6496	1.56	.2905	.1467	29.33
38A	5.0E-3	2.6471	1.57	.2661	.1352	27.04
38B		2.6471	1.48	.2692	.1289	25.79
39A		2.5806	1.69	.3984	.2179	43.58
39B		2.5806	1.58	.4115	.2104	42.08
40A		4.0862	1.28	.4582	.1898	18.98
40B		4.0862	1.52	.4485	.2206	22.06
41A	1.0E-3	1.0783	1.61	.4174	.2175	21.75
41B		1.0783	1.66	.4208	.2261	22.61
42A		3.0615	1.80	.4372	.2547	25.47
42B		3.0613	1.78	.4352	.2507	25.07



Table E-5. Nitrate Uptake Kinetic Data for Slender Wheatgrass After 17 Days (30.9% Excess 15N)

Sample Number	Concentration (Molar NO <sub>3</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basis
1		.0319	2.41	.2393	.1866	37327.70
2	5.0E-6	.0763	3.02	.1666	.1628	32565.18
3		.0393	3.48	.1628	.1833	36669.51
4		.0250	2.02	.2047	.1338	17842.24
5	7.5E-6	.0307	2.72	.2088	.1838	24506.41
6		.0604	2.61	.1840	.1554	20722.33
7		.0258	2.39	.1716	.1327	13272.62
8	1.0E-5	.0771	2.53	.1219	.0998	9980.81
9		.0395	2.99	.1787	.1729	17291.68
10		.0338	2.50	.2182	.1765	7061.49
11	2.5E-5	.0630	2.00	.1163	.0753	3011.00
12		.0395	2.89	.1450	.1356	5424.60
13		.0230	3.21	.2187	.2272	4543.86
14	5.0E-5	.0385	2.27	.1237	.0909	1817.47
15		.0579	2.63	.1988	.1692	3384.10
16		.0494	2.70	.2055	.1796	2394.17
17	7.5E-5	.0265	2.70	.1752	.1531	2041.17
18		.0324	2.96	.1954	.1872	2495.72
19		.0306	2.84	.2163	.1988	1988.00
20	1.0E-4	.0648	2.20	.2359	.1680	1679.55
21		.0554	2.45	.2397	.1901	1900.53
22		.0396	2.70	.2420	.2115	845.83
23	2.5E-4	.0529	2.50	.2302	.1862	744.98
24		.0538	2.75	.2897	.2578	1031.29
25		.0391	2.08	.3218	.2166	433.23
26	5.0E-4	.0556	1.71	.3097	.1714	342.77
27		.1142	1.94	.3162	.1985	397.04
28		.0306	2.73	.3742	.3306	440.81
29	7.5E-4	.0825	1.98	.3766	.2413	321.76
30		.0714	2.28	.3377	.2492	332.24
31		.0320	2.91	.4318	.4066	406.65
32	1.0E-3	.0608	1.63	.2893	.1526	152.61
33		.1105	2.30	.3839	.2858	285.75
34		.0477	3.10	.4913	.4929	197.16
35	2.5E-3	.0450	2.30	.5425	.4038	161.52
36		.0576	2.35	.5165	.3928	157.12
37		.0615	2.75	.6642	.5911	118.22
38	5.0E-3	.0620	2.33	.7067	.5329	106.58
39		.0689	2.49	.5766	.4646	92.93
40		.0586	2.81	.8795	.7998	79.98
41	1.0E-2	.0358	2.53	1.0401	.8516	85.16
42		.1010	1.60	.9598	.4970	49.70





Table E-6. Nitrate Uptake Kinetic Data for Slender Wheatgrass After 79 Days (30.9% Excess 15N)

Sample Number	Concentration (Molar NO <sub>3</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis	
1A		5.4728	1.87	.0188	.0114	2275.47	
1B		5.4728	1.94	.0186	.0117	2335.53	
2A	5.0E-6	8.4442	1.80	.0152	.0089	1770.87	
2B		8.4442	1.82	.0160	.0094	1884.79	
3A		4.5669	1.68	.0183	.0099	1989.90	
3B		4.5669	2.09	.0173	.0117	2340.26	
4A		6.5543	1.77	.0150	.0086	1145.63	
4B		6.5543	1.32	.0142	.0061	808.80	
5A	7.5E-6	6.0946	1.94	.0121	.0076	1012.90	
5B		6.0946	2.01	.0108	.0070	936.70	
6A		7.0366	2.24	.0121	.0088	1169.54	
6B		7.0366	2.15	.0121	.0084	1122.55	
7A		5.8425	1.71	.0096	.0053	531.26	
7B		5.8425	1.83	.0098	.0058	580.39	
8A	1.0E-5	2.3773	2.00	.0106	.0069	686.08	
8B		2.3773	1.90	.0101	.0062	621.04	
9A		6.2975	1.87	.0081	.0049	490.19	
9B		6.2975	1.80	.0085	.0050	495.15	
10A		4.1089	2.00	.0216	.0140	559.22	
10B		4.1089	2.00	.0242	.0157	626.54	
11A	2.5E-5	9.3555	2.21	.0105	.0075	300.39	
11B		9.3555	2.01	.0110	.0072	286.21	
12A		4.3667	1.86	.0089	.0054	214.29	
12B		4.3667	1.72	.0096	.0053	213.75	
13A		4.7195	2.22	.0092	.0066	132.19	
13B		4.7195	1.90	.0098	.0060	120.52	
14A	5.0E-5	5.6803	1.86	.0163	.0098	196.23	
14B		5.6803	1.90	.0164	.0101	201.68	
15A		6.7113	1.64	.0162	.0086	171.96	
15B		6.7113	1.38	.0164	.0073	146.49	
16A		4.1420	1.94	.0125	.0078	104.64	
16B		4.1420	1.87	.0141	.0085	113.77	
17A	7.5E-5	4.1553	1.88	.0226	.0138	183.34	
17B		4.1553	1.75	.0242	.0137	182.74	
18A		5.9293	1.47	.0224	.0107	142.08	
18B		5.9293	1.57	.0229	.0116	155.14	
19A		4.3776	1.92	.0119	.0074	73.94	
19B		4.3776	2.05	.0113	.0075	74.97	
20A	1.0E-4	5.4332	1.91	.0169	.0104	104.46	
20B		5.4332	1.82	.0166	.0098	97.77	



# Hofstee Plot Parameters

Sample Number	Concentration (Molar NO3)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
21A	2.5E-4	5.6615	2.02	.0203	.0133	132.71
21B		5.6615	1.85	.0185	.0111	110.76
22A		5.0693	1.81	.0270	.0158	63.26
22B		5.0693	1.75	.0267	.0151	60.49
23A	2.5E-4	6.4434	1.94	.0279	.0175	70.07
23B		6.4434	1.43	.0286	.0132	52.94
24A		7.3732	1.93	.0295	.0184	73.70
24B		7.3732	1.98	.0296	.0190	75.87
25A	5.0E-4	8.0891	1.92	.0320	.0199	39.77
25B		8.0891	2.08	.0340	.0229	45.77
26A		6.8598	1.50	.0537	.0261	52.14
26B		6.8598	1.95	.0455	.0287	57.43
27A	7.5E-4	4.4762	1.78	.0349	.0201	40.21
27B		4.4762	1.55	.0342	.0172	34.31
28A		7.0031	1.82	.0411	.0242	32.28
28B		7.0031	1.78	.0419	.0241	32.18
29A	1.0E-3	5.5055	1.69	.0430	.0235	31.36
29B		5.5055	1.63	.0419	.0221	29.47
30A		5.2723	1.81	.0375	.0220	29.29
30B		5.2723	1.85	.0382	.0229	30.49
31A	2.5E-3	6.1337	1.94	.0531	.0333	33.34
31B		6.1337	1.76	.0482	.0275	27.45
32A		6.1217	1.97	.0370	.0236	23.59
32B		6.1217	2.02	.0372	.0243	24.32
33A	5.0E-3	5.5852	1.81	.0482	.0282	28.23
33B		5.5852	1.48	.0473	.0227	22.66
34A		7.0957	1.66	.0978	.0525	21.02
34B		7.0957	1.32	.1032	.0441	17.63
35A	2.5E-3	6.4618	1.97	.0748	.0477	19.08
35B		6.4618	1.79	.0211	.0122	4.89
36A		5.5114	1.75	.0830	.0470	18.80
36B		5.5114	1.57	.0813	.0413	16.52
37A	5.0E-3	5.5151	1.66	.1858	.0998	19.96
37B		5.5151	1.72	.1840	.1024	20.48
38A		7.8794	1.88	.1060	.0645	12.90
38B		7.8794	1.81	.1152	.0675	13.50
39A	1.0E-3	7.2297	1.88	.1173	.0714	14.27
39B		7.2297	1.75	.1156	.0655	13.09
40A		8.0779	1.70	.2310	.1271	12.71
40B		8.0779	1.62	.2276	.1193	11.93
41A	1.0E-3	6.3241	1.70	.2411	.1326	13.26
41B		6.3241	1.75	.2124	.1203	12.03
42A		5.9568	1.80	.1768	.1030	10.30
42B		6.0143	1.82	.2211	.1302	13.02



Table E-7. Nitrate Uptake Kinetic Data for Magna Smooth Brome After 15 Days (35.5% Excess 15N)

Sample Number	Concentration (Molar NO <sub>3</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basals	
1		.0902	1.74	.2071	.1015	20301.63	
2	5.0E-6	.0767	3.12	.1511	.1328	26559.55	
3		.1006	1.61	.1744	.0791	15818.82	
4		.0841	2.72	.1443	.1106	14741.63	
5	7.5E-6	.0654	2.23	.1677	.1053	14045.86	
6		.0405	2.18	.1656	.1017	13558.99	
7		.0674	1.51	.1514	.0644	6439.83	
8	1.0E-5	.0797	1.97	.1678	.0931	9311.72	
9		.1009	3.01	.1607	.1363	13625.55	
10		.0431	2.89	.1720	.1400	5600.90	
11	2.5E-5	.1349	1.90	.2033	.1088	4352.34	
12		.0464	3.77	.1412	.1500	5998.02	
13		.0693	2.46	.2165	.1500	3000.51	
14	5.0E-5	.1311	2.39	.2462	.1658	3315.03	
15		.0828	3.06	.2164	.1865	3730.61	
16		.0483	3.86	.1864	.2027	2702.36	
17	7.5E-5	.0668	2.35	.2390	.1582	2109.48	
18		.0740	2.44	.2228	.1531	2041.81	
19		.0243	2.65	.2428	.1812	1812.45	
20	1.0E-4	.0249	3.71	.2956	.3089	3089.23	
21		.0917	1.79	.2260	.1140	1139.55	
22		.0522	2.87	.3154	.2550	1019.94	
23	2.5E-4	.0547	2.97	.3266	.2732	1092.96	
24		.0730	2.92	.3678	.3025	1210.11	
25		.0688	3.28	.3214	.2970	593.91	
26	5.0E-4	.0818	3.01	.2936	.2489	497.88	
27		.0482	3.08	.3871	.3359	671.70	
28		.0695	2.84	.4873	.3898	519.79	
29	7.5E-4	.0351	3.75	.4377	.4624	616.48	
30		.0539	3.22	.4335	.3932	524.27	
31		.0682	2.73	.3847	.2958	295.84	
32	1.0E-3	.0420	2.13	.3035	.1821	182.10	
33		.1033	2.79	.4741	.3726	372.60	
34		.0528	2.94	.4656	.3856	154.24	
35	2.5E-3	.0828	1.76	.3862	.1915	76.59	
36		.0961	2.91	.5047	.4137	165.48	
37		.0878	2.52	.5331	.3784	75.69	
38	5.0E-3	.0969	2.88	.6380	.5176	103.52	
39		.1318	2.66	.5612	.4205	84.10	
40		.1203	2.49	.6951	.4875	48.75	
41	1.0E-2	.0450	2.86	.7435	.5990	59.90	
42		.1418	2.39	.8877	.5976	59.76	



Table E-8. Nitrate Uptake Kinetic Data for Magna Smooth Brome After 80 Days (30.9% Excess 15N)

Sample Number	Concentration (Molar N03)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1A		12.3100	1.73	.0127	.0071	1422.10
1B		12.3100	1.69	.0120	.0066	1312.87
2A	5.0E-6	16.0100	1.64	.0159	.0085	1692.11
2B		11.8800	2.04	.0156	.0103	2065.19
3A		5.5300	1.76	.0174	.0099	1987.33
3B		5.5300	1.99	.0168	.0108	2161.08
4A		10.6000	1.74	.0269	.0151	2019.86
4B		10.6000	1.74	.0258	.0145	1934.14
5A	7.5E-6	14.5900	1.66	.0254	.0136	1812.59
5B		12.1400	2.00	.0142	.0092	1223.83
6A		6.1200	1.91	.0121	.0075	1001.09
6B		6.1200	1.87	.0095	.0058	767.10
7A		14.0400	1.74	.0227	.0128	1280.61
7B		14.0400	1.89	.0227	.0138	1384.61
8A	1.0E-5	8.9500	1.52	.0180	.0089	889.34
8B		8.9500	1.67	.0180	.0097	970.78
9A		8.5800	1.88	.0252	.0153	1533.43
9B		8.5800	1.78	.0246	.0142	1415.23
10A		12.0600	1.77	.0164	.0094	375.86
10B		12.0600	1.67	.0164	.0089	354.74
11A	2.5E-5	7.1000	2.01	.0109	.0071	284.27
11B		7.1000	2.11	.0104	.0071	285.33
12A		3.7400	2.26	.0178	.0130	519.53
12B		3.7400	2.15	.0186	.0129	517.68
13A		9.8700	1.69	.0250	.0137	273.71
13B		9.8700	1.81	.0254	.0148	296.59
14A	5.0E-5	7.0600	1.85	.0171	.0103	205.40
14B		7.0600	1.85	.0172	.0103	206.19
15A		3.8200	1.81	.0270	.0158	316.87
15B		3.8200	1.94	.0260	.0163	325.68
16A		5.4700	1.93	.0157	.0098	130.20
16B		5.4700	1.78	.0160	.0092	122.88
17A	7.5E-5	12.7600	1.76	.0343	.0195	260.51
17B		12.7600	1.75	.0332	.0188	250.49
18A		9.6700	1.83	.0294	.0174	231.96
18B		9.6700	2.06	.0286	.0191	254.79
19A		10.7800	1.78	.0285	.0164	163.73
19B		10.7800	1.85	.0286	.0172	171.63
20A	1.0E-4	12.9200	2.06	.0338	.0226	225.54
20B		12.9200	1.82	.0356	.0209	209.09





## Hofstee Plot Parameters

Sample Number	Concentration (Molar N03)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basis
21A		6.5900	2.01	.0133	.0087	86.69
21B		6.5900	1.95	.0135	.0085	85.39
22A		9.4400	1.54	.0459	.0229	91.49
22B		9.4400	1.53	.0453	.0224	89.75
23A	2.5E-4	4.5800	1.42	.0586	.0268	107.40
23B		4.5800	1.51	.0594	.0291	116.36
24A		4.6000	2.07	.0274	.0184	73.53
24B		4.6000	2.14	.0260	.0180	72.17
25A		10.4700	2.15	.0478	.0332	66.44
25B		10.4700	2.15	.0465	.0324	64.87
26A	5.0E-4	12.5100	1.93	.0552	.0345	68.93
26B		12.5100	1.74	.0539	.0304	60.82
27A		9.3300	2.12	.0333	.0229	45.72
27B		9.3300	2.14	.0335	.0232	46.35
28A		10.2100	2.22	.0441	.0317	42.23
28B		10.2100	2.13	.0414	.0286	38.11
29A	7.5E-4	24.0700	1.77	.0468	.0268	35.67
29B		24.0700	1.69	.0495	.0271	36.15
30A		11.1900	1.87	.0385	.0233	31.05
30B		11.1900	1.87	.0384	.0232	31.00
31A		15.6100	1.75	.0896	.0508	50.79
31B		15.6100	1.61	.0948	.0494	49.43
32A	1.0E-3	7.6500	1.70	.0692	.0381	38.14
32B		7.6500	1.65	.0695	.0372	37.18
33A		22.9700	1.67	.0964	.0521	52.14
33B		22.9700	1.47	.0913	.0434	43.45
34A		8.6900	2.20	.0759	.0539	21.57
34B		8.6900	2.10	.0734	.0498	19.93
35A	2.5E-3	3.8400	1.91	.0733	.0453	18.13
35B		3.8400	1.95	.0713	.0449	17.97
36A		7.0900	1.73	.1264	.0709	28.36
36B		7.0900	1.64	.1189	.0629	25.18
37A		4.9800	2.13	.1015	.0700	13.99
37B		4.9800	2.15	.1014	.0706	14.13
38A	5.0E-3	4.9000	2.16	.1187	.0829	16.57
38B		4.9000	2.14	.1161	.0806	16.12
39A		9.8600	1.70	.1181	.0649	12.97
39B		9.8600	1.76	.0805	.0460	9.19
40A		12.4700	1.61	.2095	.1090	10.90
40B		12.4700	1.49	.2239	.1082	10.82
41A	1.0E-3	11.9900	1.96	.2396	.1517	15.17
41B		11.9900	1.98	.2437	.1559	15.59
42A		13.5200	2.00	.2837	.1839	18.39
42B		13.5200	2.11	.2437	.1665	16.65



F. Ammonium Uptake Kinetic Data for Experiments Using  
Ammonium Plus Distilled Water



Table F-1. Ammonium Uptake Kinetic Data for Alpine Sheep Fescue After 78 Days Using Distilled Water (30.1% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basals
1A		1.3865	2.92	.0288	.0279	11175.55
1B		1.3865	2.54	.0259	.0219	8742.33
2A	2.5E-6	2.1370	.92	.0392	.0120	4792.56
2B		2.1370	2.07	.0360	.0248	9902.99
3A		1.6783	2.58	.0284	.0243	9737.14
3B		1.6783	2.42	.0225	.0181	7235.88
4A		1.1866	2.19	.0411	.0299	5980.66
4B		1.1866	2.94	.0326	.0318	6368.37
5A	5.0E-6	2.0219	1.61	.0565	.0302	6044.19
5B		2.0219	1.59	.0644	.0340	6803.72
6A		1.4455	1.84	.0315	.0193	3851.16
6B		1.4455	2.18	.0308	.0223	4461.40
7A		.7542	2.27	.0428	.0323	4303.70
7B		.7542	2.28	.0398	.0301	4019.67
8A	7.5E-6	1.3662	1.95	.0578	.0374	4992.69
8B		1.3662	2.47	.0524	.0430	5733.24
9A		1.4150	2.27	.0634	.0478	6375.11
9B		1.4150	2.08	.0599	.0414	5519.03
10A		1.8835	2.14	.0770	.0547	5474.42
10B		1.8835	2.39	.0742	.0589	5891.63
11A	1.0E-5	.5404	3.23	.0710	.0762	7618.94
11B		.5404	3.60	.0799	.0956	9556.15
12A		2.0015	1.84	.0623	.0381	3808.37
12B		2.0015	1.74	.0637	.0368	3682.33
13A		1.3537	3.08	.1059	.1084	4334.51
13B		1.3537	3.21	.1033	.1102	4406.55
14A	2.5E-5	.9380	2.44	.1224	.0992	3968.85
14B		.9380	2.39	.1158	.0919	3677.90
15A		.9237	1.99	.1942	.1284	5135.65
15B		.9237	2.17	.1716	.1237	4948.47
16A		.6481	2.84	.1116	.1053	2105.94
16B		.6481	2.05	.1487	.1013	2025.48
17A	5.0E-5	1.6833	1.12	.2330	.0867	1733.95
17B		1.6833	1.57	.1698	.0886	1771.34
18A		1.0088	2.37	.1323	.1042	2083.40
18B		1.0088	2.09	.1314	.0912	1824.76
19A		1.2467	2.86	.1956	.1859	2478.03
19B		1.2467	2.54	.1725	.1456	1940.86
20A	7.5E-5	.7276	2.64	.1559	.1367	1823.15
20B		.7276	2.45	.2605	.2120	2827.13



## Hofstee Plot Parameters

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
21A		1.8198	1.28	.1917	.0815	1086.94
21B		1.8198	1.13	.1844	.0692	923.02
22A		1.2884	2.37	.1638	.1290	1289.72
22B		1.2884	1.80	.2150	.1286	1285.71
23A	1.0E-4	1.8055	1.47	.2325	.1135	1135.47
23B		1.8055	1.48	.1703	.0837	837.36
24A		1.4029	1.22	.2243	.0909	909.12
24B		1.4029	2.20	.2070	.1513	1512.96
25A		.9952	2.09	.1989	.1381	552.43
25B		.9952	2.69	.1939	.1733	693.14
26A	2.5E-4	1.8634	1.39	.2381	.1100	439.81
26B		1.8634	1.98	.2847	.1873	749.11
27A		.9345	3.13	.1449	.1507	602.71
27B		.9345	2.33	.1784	.1381	552.39
28A		1.0466	3.02	.1987	.1994	398.72
28B		1.0466	1.79	.3102	.1845	368.94
29A	5.0E-4	.8430	2.29	.2908	.2212	442.48
29B		.8430	3.28	.2333	.2542	508.45
30A		.7112	1.84	.3044	.1861	372.16
30B		.7112	1.65	.3457	.1895	379.01
31A		1.4078	2.53	.3124	.2626	350.11
31B		1.4078	1.97	.2635	.1725	229.94
32A	7.5E-4	.8735	2.89	.2570	.2468	329.01
32B		.8735	2.69	.3191	.2852	380.23
33A		1.4395	2.09	.3248	.2255	300.70
33B		1.4395	2.51	.3222	.2687	358.24
34A		1.3345	2.00	.3640	.2419	241.86
34B		1.3345	1.85	.4261	.2619	261.89
35A	1.0E-3	2.6311	1.89	.4361	.2738	273.83
35B		2.6311	1.64	.4130	.2250	225.02
36A		1.3933	2.21	.4035	.2963	296.26
36B		1.3933	2.58	.3515	.3013	301.29
37A		1.1044	1.67	.5261	.2919	116.76
37B		1.1044	2.39	.4934	.3918	156.71
38A	2.5E-3	.5913	2.42	.3969	.3191	127.64
38B		.5913	2.58	.3853	.3303	132.10
39A		1.0696	2.27	.4534	.3419	136.77
39B		1.0696	1.91	.4197	.2663	106.53
40A		1.3764	1.84	.5369	.3282	65.64
40B		1.3764	1.85	.5921	.3639	72.78
41A	5.0E-3	1.4615	1.28	.5316	.2261	45.21
41B		1.4615	1.61	.5046	.2699	53.98
42A		1.3038	1.95	.5263	.3410	68.19
42B		1.3038	2.54	.4722	.3985	79.69





G. Ammonium and Nitrate Uptake by Roots and Shoots from  
Nutrient Solution



Table G-1. Ammonium Uptake Kinetic Data for Magna Smooth Brome Roots After 78 Days (30.3% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
1A		2.7958	1.02	.0292	.0098	3931.88
1B		2.7958	.81	.0279	.0075	2983.37
2A	2.5E-6	3.6686	.93	.1545	.0474	18968.32
2B		3.6686	1.01	.1458	.0486	19440.00
3A		7.1949	1.02	.0249	.0084	3352.87
3B		7.1949	1.16	.0256	.0098	3920.26
4A		7.3034	.72	.0341	.0081	1620.59
4B		7.3034	.76	.0358	.0090	1795.91
5A	5.0E-6	5.2147	1.08	.1281	.0457	9131.88
5B		5.2147	1.08	.1318	.0470	9395.64
6A		1.9049	1.06	.0671	.0235	4694.79
6B		1.9049	1.12	.0680	.0251	5027.06
7A		5.5779	.74	.0649	.0159	2113.36
7B		5.5779	.64	.0618	.0131	1740.46
8A	7.5E-6	2.1369	1.03	.1579	.0537	7156.74
8B		2.1369	1.10	.1585	.0575	7672.17
9A		3.8554	1.02	.0600	.0202	2693.07
9B		3.8554	.96	.0622	.0197	2627.59
10A		8.2904	.89	.0525	.0154	1542.08
10B		8.2904	.73	.0575	.0139	1385.31
11A	1.0E-5	1.8839	.81	.1139	.0304	3044.85
11B		1.8839	.90	.1108	.0329	3291.09
12A		3.7137	.97	.1539	.0493	4926.83
12B		3.7137	.89	.1481	.0435	4350.13
13A		5.2514	.80	.1063	.0281	1122.64
13B		5.2514	.97	.1022	.0327	1308.70
14A	2.5E-5	4.2900	.76	.1363	.0342	1367.50
14B		4.2900	.79	.1294	.0337	1349.52
15A		4.6785	1.26	.1528	.0635	2541.62
15B		4.6785	1.18	.1525	.0594	2375.58
16A		2.5560	.81	.1611	.0431	861.33
16B		2.5560	.94	.1570	.0487	974.13
17A	5.0E-5	7.6341	.91	.1733	.0520	1040.94
17B		7.6341	.97	.1676	.0537	1073.08
18A		6.6911	1.15	.1446	.0549	1097.62
18B		6.6911	1.16	.1422	.0544	1088.79
19A		4.4342	1.18	.3326	.1295	1727.03
19B		4.4342	1.11	.3282	.1202	1603.09
20A	7.5E-5	3.5291	1.15	.2696	.1023	1364.31
20B		3.5291	1.09	.3050	.1097	1462.93



## Hofstee Plot Parameters

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basis
21A		3.6151	1.17	.1673	.0646	861.35
21B		3.6151	1.08	.1732	.0617	823.13
22A		6.7046	1.04	.3063	.1051	1051.33
22B		6.7046	.99	.2835	.0926	926.29
23A	1.0E-4	4.2145	1.13	.2804	.1046	1045.72
23B		4.2145	1.19	.2827	.1110	1110.27
24A		4.7490	.88	.3936	.1143	1143.13
24B		4.7490	.91	.4011	.1205	1204.62
25A		5.7624	.72	.3553	.0844	337.71
25B		5.7624	.86	.3437	.0976	390.21
26A	2.5E-4	5.6033	.87	.3841	.1103	441.14
26B		5.6033	.87	.3524	.1012	404.74
27A		6.4474	.74	.3353	.0819	327.55
27B		6.4474	.60	.3918	.0776	310.34
28A		2.7529	1.04	.5930	.2035	407.08
28B		2.7529	.96	.5942	.1883	376.52
29A	5.0E-4	3.6769	.96	.4932	.1563	312.52
29B		3.6769	.95	.4923	.1544	308.70
30A		3.1011	1.19	.4490	.1763	352.68
30B		3.1011	1.13	.4172	.1556	311.18
31A		4.0189	.87	.4519	.1298	173.00
31B		4.0189	.86	.4479	.1271	169.50
32A	7.5E-4	1.7710	1.31	.5711	.2469	329.21
32B		1.7710	1.30	.5577	.2393	319.04
33A		3.4751	1.10	.7630	.2770	369.33
33B		3.4751	1.20	.8117	.3215	428.62
34A		2.2971	1.06	.5716	.2000	199.97
34B		2.2971	1.12	.5529	.2044	204.37
35A	1.0E-3	2.5232	.94	.5924	.1838	183.78
35B		2.5232	.91	.5664	.1701	170.11
36A		5.6504	1.03	.8066	.2742	274.19
36B		5.6504	.87	.7809	.2242	224.22
37A		2.0482	1.10	.7125	.2587	103.47
37B		2.0482	1.11	.7077	.2593	103.70
38A	2.5E-3	3.7570	1.00	.7264	.2397	95.89
38B		3.7570	1.09	.7239	.2604	104.17
39A		2.8024	1.10	1.0712	.3889	155.55
39B		2.8024	1.11	1.0290	.3770	150.78
40A		7.8677	.86	.7569	.2148	42.97
40B		7.8677	.96	.7581	.2402	48.04
41A	5.0E-3	8.5741	.77	1.1657	.2962	59.25
41B		8.5741	.83	1.1285	.3091	61.83
42A		3.4272	1.08	1.4202	.5062	101.24
42B		3.4272	.96	1.3890	.4401	88.02



Table G-2. Ammonium Uptake Kinetic Data for Magna Smooth Brome Shoots After 78 Days (30.3% Excess 15N)

Sample Number	Concentration (Molar NH <sub>4</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters		
					mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basis	
1A		6.2265	2.18	.0182	.0131	5237.76	
1B		6.2265	2.16	.0148	.0106	4220.20	
2A	2.5E-6	9.5511	2.01	.0124	.0082	3290.30	
2B		9.5511	2.04	.0113	.0076	3043.17	
3A		18.1893	1.66	.0095	.0052	2081.85	
3B		18.1893	1.66	.0091	.0050	1994.19	
4A		10.6053	1.69	.0091	.0051	1015.12	
4B		10.6053	1.71	.0089	.0050	1004.55	
5A	5.0E-6	10.9718	1.89	.0109	.0068	1359.80	
5B		10.9718	1.87	.0106	.0065	1308.38	
6A		4.3952	1.81	.0102	.0061	1218.61	
6B		4.3952	1.95	.0097	.0062	1248.51	
7A		7.8377	2.12	.0096	.0067	895.58	
7B		7.8377	2.31	.0093	.0071	945.35	
8A	7.5E-6	5.8967	1.87	.0117	.0072	962.77	
8B		5.8967	2.28	.0116	.0087	1163.83	
9A		9.4929	1.61	.0127	.0067	899.76	
9B		9.4929	2.10	.0099	.0069	914.85	
10A		17.0954	1.32	.0122	.0053	531.49	
10B		17.0954	1.49	.0113	.0056	555.68	
11A	1.0E-5	5.3693	1.69	.0114	.0064	635.84	
11B		5.3693	1.59	.0102	.0054	535.25	
12A		11.5732	1.71	.0000	.0000	.00	
12B		11.5732	1.92	.0000	.0000	.00	
13A		13.9788	1.83	.0000	.0000	.00	
13B		13.9788	1.84	.0102	.0062	247.76	
14A	2.5E-5	10.4873	1.77	.0108	.0063	252.36	
14B		10.4873	1.81	.0107	.0064	255.67	
15A		11.7006	1.87	.0110	.0068	271.55	
15B		11.7006	2.17	.0109	.0078	312.25	
16A		5.6720	2.69	.0124	.0110	220.17	
16B		5.6720	2.69	.0120	.0107	213.07	
17A	5.0E-5	10.5411	2.23	.0135	.0099	198.71	
17B		10.5411	2.55	.0122	.0103	205.35	
18A		11.3825	1.31	.0124	.0054	107.22	
18B		11.3825	1.68	.0120	.0067	133.07	
19A		10.4960	1.84	.0113	.0069	91.49	
19B		10.4960	1.72	.0111	.0063	84.01	
20A	7.5E-5	11.1655	2.19	.0125	.0090	120.46	
20B		11.1655	1.93	.0143	.0091	121.45	





Hofstee Plot Parameters

Sample Number	Concentration (Molar NH4)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
21A		7.9052	1.90	.0148	.0093	123.74
21B		7.9052	1.88	.0153	.0095	126.57
22A		15.5204	1.74	.0167	.0096	95.90
22B		15.5204	1.64	.0179	.0097	96.88
23A	1.0E-4	8.6867	2.53	.0118	.0099	98.53
23B		8.6867	2.44	.0127	.0102	102.27
24A		16.3474	1.69	.0102	.0057	56.89
24B		16.3474	1.61	.0104	.0055	55.26
25A		13.2291	1.85	.0188	.0115	45.91
25B		13.2291	2.01	.0186	.0123	49.35
26A	2.5E-4	10.1813	1.80	.0166	.0099	39.45
26B		10.1813	1.93	.0173	.0110	44.08
27A		10.0750	1.84	.0520	.0316	126.31
27B		10.0750	1.85	.0501	.0306	122.36
28A		5.6229	2.26	.0281	.0210	41.92
28B		5.6229	2.33	.0302	.0232	46.45
29A	5.0E-4	6.5225	1.81	.0337	.0201	40.26
29B		6.5225	1.92	.0340	.0215	43.09
30A		8.7805	1.71	.0170	.0096	19.19
30B		8.7805	1.57	.0182	.0094	18.86
31A		7.3878	2.69	.0182	.0162	21.54
31B		7.3878	2.63	.0198	.0172	22.91
32A	7.5E-4	4.3800	2.28	.0288	.0217	28.90
32B		4.3800	2.33	.0294	.0226	30.14
33A		8.6937	1.70	.0206	.0116	15.41
33B		8.6937	1.91	.0213	.0134	17.90
34A		4.3018	2.51	.0251	.0208	20.79
34B		4.3018	2.41	.0256	.0204	20.36
35A	1.0E-3	6.6441	2.23	.0320	.0236	23.55
35B		6.6441	2.27	.0323	.0242	24.20
36A		9.2053	2.00	.0230	.0152	15.18
36B		9.2053	1.87	.0282	.0174	17.40
37A		6.9844	2.44	.0410	.0330	13.21
37B		6.9844	2.31	.0444	.0338	13.54
38A	2.5E-3	6.2152	2.41	.0371	.0295	11.80
38B		6.2152	2.32	.0376	.0288	11.52
39A		9.3752	1.45	.0455	.0218	8.71
39B		9.3752	1.45	.0453	.0217	8.67
40A		15.0826	1.67	.0752	.0414	8.29
40B		15.0826	1.78	.0837	.0492	9.83
41A	5.0E-3	17.3538	1.96	.0643	.0416	8.32
41B		17.3538	1.78	.0708	.0416	8.32
42A		10.5714	1.73	.0735	.0420	8.39
42B		10.5714	1.29	.0936	.0398	7.97



Table G-3. Nitrate Uptake Kinetic Data for Magna Smooth Brome Roots After 80 Days (30.9% Excess 15N)

Sample Number	Concentration (Molar ND3)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basis
1A		5.5600	1.13	.0250	.0091	1828.48
1B		5.5600	1.05	.0223	.0076	1515.53
2A	5.0E-6	5.5600	1.01	.0242	.0079	1582.01
2B		1.4300	1.02	.0488	.0161	3221.75
3A		1.4300	.85	.0456	.0125	2508.74
3B		1.4300	.97	.0461	.0145	2894.30
4A		3.8500	.89	.0607	.0175	2331.09
4B		3.8500	.90	.0560	.0163	2174.76
5A	7.5E-6	3.8500	.61	.0613	.0121	1613.51
5B		1.4000	1.14	.0387	.0143	1903.69
6A		1.4000	1.24	.0379	.0152	2027.87
6B		1.4000	1.12	.0416	.0151	2010.44
7A		5.3000	.84	.0402	.0109	1092.82
7B		5.3000	.97	.0405	.0127	1271.36
8A	1.0E-5	3.6100	.98	.0366	.0116	1160.78
8B		3.6100	.98	.0365	.0116	1157.61
9A		2.3300	1.01	.0589	.0193	1925.21
9B		2.3300	1.10	.0568	.0202	2022.01
10A		3.6900	1.21	.0372	.0146	582.68
10B		3.6900	1.09	.0372	.0131	524.89
11A	2.5E-5	1.4400	.86	.0382	.0106	425.27
11B		1.4400	1.14	.0369	.0136	544.54
12A		.4500	1.07	.0549	.0190	760.43
12B		.4500	1.21	.0558	.0219	874.02
13A		3.9300	.75	.0514	.0125	249.51
13B		3.9300	.82	.0522	.0139	277.05
14A	5.0E-5	1.6800	1.29	.0540	.0225	450.87
14B		1.6800	1.30	.0532	.0224	447.64
15A		.7500	.38	.0710	.0087	174.63
15B		.7500	.99	.0655	.0210	419.71
16A		1.0600	1.42	.0479	.0220	293.50
16B		1.0600	1.38	.0483	.0216	287.61
17A	7.5E-5	4.7100	.96	.0768	.0239	318.14
17B		4.7100	1.03	.0735	.0245	326.67
18A		2.7000	1.16	.0675	.0253	337.86
18B		2.7000	1.12	.0676	.0245	326.70
19A		3.6600	1.09	.0646	.0228	227.88
19B		3.6600	1.00	.0645	.0209	208.74
20A	1.0E-4	4.8500	1.08	.0668	.0233	233.48
20B		4.8500	.96	.0700	.0217	217.48



Hofstee Plot Parameters

Sample Number	Concentration (Molar NO3)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
21A		1.5400	1.36	.0301	.0132	132.48
21B		1.5400	1.03	.0307	.0102	102.33
22A		3.7800	.82	.0841	.0223	89.27
22B		3.7800	.87	.0828	.0233	93.25
23A	2.5E-4	2.1500	.78	.0922	.0233	93.10
23B		2.1500	.85	.0923	.0254	101.56
24A		1.3600	1.12	.0711	.0258	103.08
24B		1.3600	1.05	.0678	.0230	92.16
25A		2.7000	1.31	.1211	.0513	102.68
25B		2.7000	1.36	.1148	.0505	101.05
26A	5.0E-4	4.0200	1.12	.1147	.0416	83.15
26B		4.0200	.86	.1104	.0307	61.45
27A		1.7700	1.33	.0997	.0429	85.83
27B		1.7700	1.26	.0995	.0406	81.15
28A		1.8100	1.21	.1255	.0491	65.53
28B		1.8100	1.16	.1173	.0440	58.71
29A	7.5E-4	4.0700	1.07	.1409	.0488	65.05
29B		4.0700	1.12	.1417	.0514	68.48
30A		2.5300	1.46	.0966	.0456	60.86
30B		2.5300	1.40	.0934	.0423	56.42
31A		8.0700	.96	.1414	.0439	43.93
31B		8.0700	.94	.1486	.0452	45.21
32A	1.0E-3	1.6900	1.29	.1927	.0804	80.45
32B		1.6900	1.24	.1937	.0777	77.73
33A		12.8100	1.07	.1488	.0515	51.53
33B		12.8100	.75	.1393	.0338	33.81
34A		2.5100	1.20	.1118	.0434	17.37
34B		2.5100	1.06	.1105	.0379	15.16
35A	2.5E-3	.8600	1.32	.1413	.0604	24.14
35B		.8600	1.31	.1439	.0610	24.40
36A		3.0300	.96	.2225	.0691	27.65
36B		3.0300	.80	.2054	.0532	21.27
37A		1.6200	1.28	.1008	.0418	8.35
37B		1.6200	1.33	.1024	.0441	8.82
38A	5.0E-3	1.4000	1.30	.1937	.0815	16.30
38B		1.4000	1.38	.1862	.0832	16.63
39A		2.8900	1.09	.1956	.0690	13.80
39B		2.8900	1.12	.1894	.0686	13.73
40A		3.1400	1.01	.1969	.0644	6.44
40B		3.1400	.82	.1814	.0481	4.81
41A	1.0E-3	4.9000	.78	.3184	.0804	8.04
41B		4.9000	.96	.3356	.1043	10.43
42A		4.6500	1.17	.2791	.1057	10.57
42B		4.6500	1.16	.2638	.0990	9.90



Table G-4. Nitrate Uptake Kinetic Data for Magna Smooth Brome Shoots After 80 Days (30.9% Excess 15N)

Sample Number	Concentration (Molar NO <sub>3</sub> )	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	Hofstee Plot Parameters	
					mg. N Taken up/ g. Plant/ 2 hr.	v/S /g. Plant Basis
1A		6.7500	2.22	.0026	.0019	373.59
1B		6.7500	2.22	.0035	.0025	502.91
2A	5.0E-6	10.4500	1.98	.0115	.0074	1473.79
2B		10.4500	2.18	.0111	.0078	1566.21
3A		4.1000	2.08	.0076	.0051	1023.17
3B		4.1000	2.34	.0066	.0050	999.61
4A		6.7500	2.22	.0077	.0055	737.61
4B		6.7500	2.22	.0085	.0061	814.24
5A	7.5E-6	10.7400	2.03	.0125	.0082	1094.93
5B		10.7400	2.11	.0110	.0075	1001.51
6A		4.7200	2.11	.0045	.0031	409.71
6B		4.7200	2.09	.0000	.0000	.00
7A		8.7400	2.29	.0121	.0090	896.73
7B		8.7400	2.44	.0119	.0094	939.68
8A	1.0E-5	5.3400	1.89	.0055	.0034	336.41
8B		5.3400	2.13	.0055	.0038	379.13
9A		6.2500	2.20	.0127	.0090	904.21
9B		6.2500	2.03	.0126	.0083	827.77
10A		8.3700	2.01	.0073	.0047	189.94
10B		8.3700	1.92	.0073	.0045	181.44
11A	2.5E-5	5.6600	2.30	.0040	.0030	119.09
11B		5.6600	2.36	.0037	.0028	113.04
12A		3.2900	2.42	.0127	.0099	397.85
12B		3.2900	2.28	.0135	.0100	398.45
13A		5.9400	2.31	.0076	.0057	113.63
13B		5.9400	2.46	.0076	.0061	121.01
14A	5.0E-5	5.3800	2.03	.0056	.0037	73.58
14B		5.3800	2.02	.0060	.0039	78.45
15A		3.0700	2.16	.0163	.0114	227.88
15B		3.0700	2.17	.0163	.0114	228.94
16A		4.4100	2.05	.0079	.0052	69.88
16B		4.4100	1.88	.0082	.0050	66.52
17A	7.5E-5	8.0500	2.23	.0094	.0068	90.45
17B		8.0500	2.17	.0096	.0067	89.89
18A		6.9700	2.09	.0146	.0099	131.67
18B		6.9700	2.43	.0135	.0106	141.55
19A		7.1200	2.13	.0099	.0068	68.24
19B		7.1200	2.29	.0102	.0076	75.59
20A	1.0E-4	8.0700	2.65	.0140	.0120	120.06
20B		8.0700	2.33	.0149	.0112	112.35





Hofstee Plot Parameters

Sample Number	Concentration (Molar N03)	Weight of Sample (g.)	Percent N in Sample	Percent Excess 15N in Sample	mg. N Taken up/ g. Plant/ 2 hr.	v/s /g. Plant Basis
21A		5.0500	2.21	.0082	.0059	58.65
21B		5.0500	2.23	.0083	.0060	59.90
22A		5.6600	2.02	.0204	.0133	53.34
22B		5.6600	1.97	.0203	.0129	51.77
23A	2.5E-4	2.4300	1.98	.0288	.0185	73.82
23B		2.4300	2.10	.0303	.0206	82.37
24A		3.2400	2.47	.0091	.0073	29.10
24B		3.2400	2.60	.0085	.0072	28.61
25A		7.7700	2.44	.0223	.0176	35.22
25B		7.7700	2.43	.0228	.0179	35.86
26A	5.0E-4	8.4900	2.31	.0271	.0203	40.52
26B		8.4900	2.16	.0272	.0190	38.03
27A		7.5600	2.31	.0177	.0132	26.46
27B		7.5600	2.34	.0181	.0137	27.41
28A		8.4000	2.44	.0265	.0209	27.90
28B		8.4000	2.34	.0251	.0190	25.34
29A	7.5E-4	20.0000	1.91	.0276	.0171	22.75
29B		20.0000	1.81	.0307	.0180	23.98
30A		8.6600	1.99	.0215	.0138	18.46
30B		8.6600	2.01	.0223	.0145	19.34
31A		7.5400	2.60	.0341	.0287	28.69
31B		7.5400	2.33	.0372	.0281	28.05
32A	1.0E-3	5.9600	1.82	.0342	.0201	20.14
32B		5.9600	1.77	.0343	.0196	19.65
33A		10.1600	2.43	.0303	.0238	23.83
33B		10.1600	2.38	.0307	.0236	23.65
34A		6.1800	2.60	.0613	.0516	20.63
34B		6.1800	2.52	.0583	.0475	19.02
35A	2.5E-3	2.9800	2.08	.0537	.0361	14.46
35B		2.9800	2.13	.0504	.0347	13.90
36A		4.0600	2.31	.0547	.0409	16.36
36B		4.0600	2.26	.0543	.0397	15.89
37A		3.3600	2.54	.1018	.0837	16.74
37B		3.3600	2.55	.1009	.0833	16.65
38A	5.0E-3	3.5000	2.50	.0887	.0718	14.35
38B		3.5000	2.45	.0881	.0699	13.97
39A		6.9700	1.95	.0859	.0542	10.84
39B		6.9700	2.03	.0354	.0233	4.65
40A		9.3300	1.81	.2137	.1252	12.52
40B		9.3300	1.72	.2382	.1326	13.26
41A	1.0E-3	7.0900	2.77	.1851	.1659	16.59
41B		7.0900	2.68	.1802	.1563	15.63
42A		8.8700	2.44	.2861	.2259	22.59
42B		8.8700	2.61	.2332	.1970	19.70



## H. Statistical Summaries for Ammonium Uptake Studies



Table H-1. Statistical Data for Fescue at 15 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
FSWT		.0098	.0000	.0031
FSTN		4.4164	.4446	.6668
FSXN	1	.0288	.0002	.0141
FSXN	2	.0314	.0011	.0330
FSXN	3	.0500	.0004	.0206
FSXN	4	.0511	.0003	.0175
FSXN	5	.0982	.0023	.0483
FSXN	6	.1107	.0011	.0339
FSXN	7	.1361	.0015	.0381
FSXN	8	.1504	.0040	.0636
FSXN	9	.1271	.0004	.0196
FSXN	10	.1699	.0023	.0484
FSXN	11	.2239	.0031	.0554
FSXN	12	.2447	.0005	.0226
FSXN	13	.3174	.0055	.0738
FSXN	14	.3576	.0005	.0221

Table H-2. Statistical Data For Fescue at 50 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
IFWT		.2464	.0020	.0450
IFTN		1.5602	.0499	.2233
IFXN	1	.0157	.0000	.0016
IFXN	2	.0287	.0000	.0024
IFXN	3	.0364	.0000	.0050
IFXN	4	.0413	.0018	.0423
IFXN	5	.0605	.0037	.0609
IFXN	6	.0923	.0001	.0105
IFXN	7	.1342	.0016	.0394
IFXN	8	.1512	.0008	.0288
IFXN	9	.2937	.0146	.1210
IFXN	10	.2977	.0062	.0788
IFXN	11	.3909	.1650	.4062
IFXN	12	.4423	.2075	.4555
IFXN	13	.5764	.0041	.0643
IFXN	14	.6205	.0034	.0585



Table H-3. Statistical Data For Fescue at 78 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
FMWT		1.9940	.3692	.6076
FMTN		1.5825	.1160	.3406
FMXN	1	.0833	.0008	.0287
FMXN	2	.0657	.0003	.0183
FMXN	3	.0955	.0011	.0329
FMXN	4	.1066	.0020	.0444
FMXN	5	.1116	.0001	.0085
FMXN	6	.1594	.0001	.0074
FMXN	7	.2199	.0016	.0395
FMXN	8	.2627	.0029	.0543
FMXN	9	.3784	.0031	.0560
FMXN	10	.4496	.0033	.0573
FMXN	11	.5938	.0158	.1258
FMXN	12	.6975	.0047	.0685
FMXN	13	.7297	.0022	.0471
FMXN	14	.7720	.0014	.0370

Table H-4. Statistical Data For Fescue at 99 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
IIFWT		1.7412	.1684	.4104
IIFTN		1.7557	.0650	.2550
IIFXN	1	.0122	.0000	.0055
IIFXN	2	.0189	.0002	.0131
IIFXN	3	.0119	.0000	.0047
IIFXN	4	.0112	.0000	.0047
IIFXN	5	.0267	.0002	.0136
IIFXN	6	.0318	.0001	.0073
IIFXN	7	.0519	.0006	.0238
IIFXN	8	.0356	.0002	.0133
IIFXN	9	.0569	.0003	.0168
IIFXN	10	.0716	.0001	.0119
IIFXN	11	.0805	.0004	.0188
IIFXN	12	.1717	.0149	.1219
IIFXN	13	.2481	.0002	.0134
IIFXN	14	.2657	.0052	.0722





Table H-5. Statistical Data For Needlegrass at 15 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
SSWT		.0269	.0000	.0056
SSTN		3.5843	.0732	.2705
SSXN	1	.0285	.0000	.0028
SSXN	2	.0367	.0000	.0049
SSXN	3	.0394	.0001	.0096
SSXN	4	.0496	.0001	.0101
SSXN	5	.0708	.0001	.0083
SSXN	6	.0873	.0000	.0022
SSXN	7	.1145	.0025	.0504
SSXN	8	.1383	.0004	.0204
SSXN	9	.1301	.0004	.0202
SSXN	10	.1472	.0011	.0339
SSXN	11	.2089	.0003	.0159
SSXN	12	.2644	.0117	.1082
SSXN	13	.3497	.0027	.0522
SSXN	14	.4621	.0034	.0586

Table H-6. Statistical Data For Needlegrass at 41 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
ISWT		.2224	.0061	.0779
ISTN		1.7657	.0880	.2967
ISXN	1	.0294	.0000	.0032
ISXN	2	.0284	.0000	.0026
ISXN	3	.0456	.0001	.0085
ISXN	4	.0502	.0000	.0033
ISXN	5	.0970	.0002	.0147
ISXN	6	.0667	.0034	.0583
ISXN	7	.1599	.0002	.0145
ISXN	8	.3043	.0001	.0114
ISXN	9	.2400	.0000	.0042
ISXN	10	.2862	.0001	.0072
ISXN	11	.1361	.0008	.0281
ISXN	12	.2016	.0306	.1748
ISXN	13	.3758	.0002	.0154
ISXN	14	.5195	.0007	.0259



Table H-7. Statistical Data For Needlegrass at 78 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
SMWT	4.9708	3.4490	1.8572
SMTN	1.5079	.0826	.2874
SMXN 1	.0292	.0001	.0088
SMXN 2	.0297	.0000	.0065
SMXN 3	.0389	.0000	.0028
SMXN 4	.0391	.0000	.0052
SMXN 5	.0521	.0001	.0085
SMXN 6	.0731	.0023	.0475
SMXN 7	.1001	.0010	.0323
SMXN 8	.0940	.0004	.0206
SMXN 9	.1403	.0023	.0478
SMXN 10	.1318	.0006	.0239
SMXN 11	.1662	.0036	.0599
SMXN 12	.1844	.0008	.0286
SMXN 13	.2082	.0026	.0510
SMXN 14	.3352	.0020	.0449

Table H-8. Statistical Data For Needlegrass at 87 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
IISWT	4.2316	1.8307	1.3530
IISTN	1.6629	.0092	.0959
IISXN 1	.0203	.0003	.0180
IISXN 2	.0105	.0000	.0044
IISXN 3	.0090	.0000	.0019
IISXN 4	.0115	.0000	.0017
IISXN 5	.0203	.0000	.0048
IISXN 6	.0275	.0000	.0017
IISXN 7	.0309	.0001	.0081
IISXN 8	.0518	.0000	.0063
IISXN 9	.0741	.0001	.0117
IISXN 10	.1167	.0000	.0008
IISXN 11	.1014	.0001	.0118
IISXN 12	.1179	.0011	.0337
IISXN 13	.1567	.0007	.0271
IISXN 14	.1611	.0072	.0851



Table H-9. Statistical Data For Wheatgrass at 15 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
ASWT		.0675	.0002	.0126
ASTN		3.2148	.1467	.3830
ASXN	1	.0820	.0014	.0367
ASXN	2	.1293	.0003	.0162
ASXN	3	.1352	.0004	.0206
ASXN	4	.2004	.0003	.0162
ASXN	5	.3096	.0051	.0714
ASXN	6	.3479	.0019	.0440
ASXN	7	.3448	.0062	.0788
ASXN	8	.4399	.0002	.0125
ASXN	9	.4969	.0032	.0562
ASXN	10	.5148	.0089	.0942
ASXN	11	.5488	.0368	.1919
ASXN	12	.6469	.0043	.0655
ASXN	13	.7359	.0546	.2336
ASXN	14	.8245	.0240	.1549

Table H-10. Statistical Data For Wheatgrass at 58 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
IAWT		2.3269	.1321	.3635
IATN		1.5176	.0477	.2185
IAXN	1	.0576	.0002	.0149
IAXN	2	.0341	.0000	.0056
IAXN	3	.0451	.0001	.0088
IAXN	4	.0500	.0001	.0082
IAXN	5	.1018	.0009	.0301
IAXN	6	.1268	.0007	.0261
IAXN	7	.1352	.0000	.0011
IAXN	8	.1413	.0005	.0217
IAXN	9	.4177	.0390	.1974
IAXN	10	.4208	.0011	.0337
IAXN	11	.3179	.0074	.0860
IAXN	12	.3288	.0001	.0110
IAXN	13	.3773	.0137	.1170
IAXN	14	.4450	.0043	.0659



Table H-11. Statistical Data For Wheatgrass at 78 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
AMWT		8.9793	4.2493	2.0614
AMTN		2.0742	.0401	.2001
AMXN	1	.0105	.0000	.0019
AMXN	2	.0098	.0000	.0014
AMXN	3	.0141	.0000	.0015
AMXN	4	.0144	.0000	.0023
AMXN	5	.0207	.0000	.0027
AMXN	6	.0283	.0000	.0050
AMXN	7	.0290	.0000	.0046
AMXN	8	.0346	.0000	.0054
AMXN	9	.0389	.0000	.0070
AMXN	10	.0455	.0001	.0112
AMXN	11	.0532	.0001	.0118
AMXN	12	.0561	.0002	.0134
AMXN	13	.0663	.0000	.0038
AMXN	14	.0979	.0001	.0091

Table H-12. Statistical Data For Brome at 15 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
BSWT		.0878	.0007	.0265
BSTN		2.2852	.0846	.2909
BSXN	1	.0683	.0001	.0100
BSXN	2	.1105	.0003	.0184
BSXN	3	.1524	.0008	.0275
BSXN	4	.1764	.0009	.0292
BSXN	5	.3437	.0011	.0329
BSXN	6	.3960	.0031	.0554
BSXN	7	.4151	.0002	.0154
BSXN	8	.4804	.0011	.0335
BSXN	9	.6364	.0117	.1080
BSXN	10	.7783	.0195	.1397
BSXN	11	.8446	.0203	.1427
BSXN	12	.7408	.0107	.1036
BSXN	13	1.0683	.0023	.0481
BSXN	14	1.3326	.0639	.2528





Table H-13. Statistical Data For Brome at 78 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
BMWT		14.2652	28.2990	5.3197
BMTN		1.6483	.0559	.2364
BMXN	1	1.6706	.0192	.1387
BMXN	2	1.5240	.0294	.1714
BMXN	3	1.6641	.0339	.1841
BMXN	4	1.4156	.0332	.1821
BMXN	5	1.6208	.0229	.1512
BMXN	6	1.7588	.1251	.3537
BMXN	7	1.6919	.0186	.1365
BMXN	8	1.6729	.0875	.2958
BMXN	9	1.4941	.0113	.1063
BMXN	10	1.6403	.0335	.1830
BMXN	11	1.8875	.0471	.2170
BMXN	12	1.8096	.0414	.2035
BMXN	13	1.7751	.1088	.3299
BMXN	14	1.4506	.0184	.1357

Table H-14. Statistical Data For Brome at 87 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
IIBWT		5.8159	3.9636	1.9909
IIBTN		1.7171	.0895	.2992
IIBXN	1	.0114	.0000	.0029
IIBXN	2	.0111	.0000	.0024
IIBXN	3	.0101	.0000	.0021
IIBXN	4	.0125	.0000	.0018
IIBXN	5	.0209	.0001	.0099
IIBXN	6	.0409	.0001	.0095
IIBXN	7	.0388	.0000	.0040
IIBXN	8	.0437	.0000	.0033
IIBXN	9	.0552	.0002	.0151
IIBXN	10	.1027	.0001	.0093
IIBXN	11	.0798	.0007	.0255
IIBXN	12	.0673	.0004	.0210
IIBXN	13	.1258	.0028	.0528



## I. Statistical Summaries for Nitrate Uptake Studies



Table I-1. Statistical Data For Fescue at 16 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
SFWT	.0241	.0001	.0076
SFTN	4.0336	.0541	.2325
SFXN 1	.0731	.0000	.0051
SFXN 2	.1150	.0003	.0162
SFXN 3	.1162	.0002	.0150
SFXN 4	.1223	.0007	.0258
SFXN 5	.1384	.0004	.0209
SFXN 6	.1574	.0011	.0330
SFXN 7	.1487	.0014	.0373
SFXN 8	.1637	.0007	.0258
SFXN 9	.1888	.0003	.0177
SFXN 10	.2103	.0005	.0221
SFXN 11	.1902	.0011	.0330
SFXN 12	.2345	.0010	.0315
SFXN 13	.3003	.0006	.0253
SFXN 14	.3312	.0005	.0233

Table I-2. Statistical Data For Fescue at 79 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
MFWT	1.4706	.1358	.3685
MFTN	1.6561	.1786	.4227
MFXN 1	.0592	.0003	.0178
MFXN 2	.0562	.0001	.0081
MFXN 3	.0538	.0002	.0134
MFXN 4	.0772	.0007	.0271
MFXN 5	.1071	.0004	.0191
MFXN 6	.0944	.0004	.0189
MFXN 7	.0887	.0006	.0253
MFXN 8	.1233	.0002	.0142
MFXN 9	.1311	.0003	.0182
MFXN 10	.1357	.0008	.0290
MFXN 11	.1925	.0081	.0900
MFXN 12	.2668	.0033	.0573
MFXN 13	.2993	.0012	.0351
MFXN 14	.4233	.0072	.0850



Table I-3. Statistical Data For Needlegrass at 15 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
SSWT	.0241	.0000	.0060
SSTN	2.6421	.1214	.3484
SSXN 1	.2042	.0043	.0659
SSXN 2	.1614	.0010	.0317
SSXN 3	.1992	.0045	.0671
SSXN 4	.2231	.0039	.0623
SSXN 5	.2546	.0033	.0575
SSXN 6	.2339	.0097	.0987
SSXN 7	.2299	.0058	.0760
SSXN 8	.3041	.0007	.0273
SSXN 9	.2948	.0041	.0638
SSXN 10	.3347	.0009	.0301
SSXN 11	.3468	.0011	.0336
SSXN 12	.4652	.0140	.1185
SSXN 13	.4816	.0098	.0992
SSXN 14	.7979	.0010	.0309

Table I-4. Statistical Data For Needlegrass at 84 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
MSWT	3.0614	1.8465	1.3588
MSTN	1.7865	.0725	.2692
MSXN 1	.0580	.0013	.0360
MSXN 2	.0251	.0002	.0129
MSXN 3	.0353	.0001	.0115
MSXN 4	.0457	.0001	.0074
MSXN 5	.0646	.0000	.0058
MSXN 6	.0559	.0002	.0145
MSXN 7	.0629	.0002	.0154
MSXN 8	.0884	.0002	.0130
MSXN 9	.1042	.0008	.0284
MSXN 10	.1179	.0004	.0205
MSXN 11	.1396	.0009	.0307
MSXN 12	.1746	.0002	.0129
MSXN 13	.3207	.0044	.0661
MSXN 14	.4362	.0002	.0157





Table I-5. Statistical Data For Wheatgrass at 17 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
SAWT		.0524	.0005	.0223
SATN		2.5069	.1764	.4200
SAXN	1	.1896	.0019	.0431
SAXN	2	.1992	.0002	.0133
SAXN	3	.1574	.0010	.0309
SAXN	4	.1598	.0028	.0525
SAXN	5	.1804	.0025	.0501
SAXN	6	.1920	.0002	.0154
SAXN	7	.2306	.0002	.0126
SAXN	8	.2540	.0010	.0315
SAXN	9	.3159	.0000	.0061
SAXN	10	.3628	.0005	.0218
SAXN	11	.3683	.0053	.0725
SAXN	12	.5168	.0007	.0256
SAXN	13	.6492	.0044	.0663
SAXN	14	.9598	.0064	.0803

Table I-6. Statistical Data For Wheatgrass at 79 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment		Mean	Variance	Std. Dev.
MAWT		5.9843	1.8390	1.3561
MATN		1.8193	.0357	.1888
MAXN	1	.0174	.0000	.0015
MAXN	2	.0127	.0000	.0016
MAXN	3	.0094	.0000	.0010
MAXN	4	.0143	.0000	.0068
MAXN	5	.0140	.0000	.0035
MAXN	6	.0198	.0000	.0051
MAXN	7	.0159	.0000	.0036
MAXN	8	.0282	.0000	.0012
MAXN	9	.0390	.0001	.0086
MAXN	10	.0406	.0000	.0022
MAXN	11	.0452	.0000	.0066
MAXN	12	.0769	.0009	.0293
MAXN	13	.1373	.0014	.0371
MAXN	14	.2183	.0005	.0225



Table I-7. Statistical Data For Brome at 15 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
SBWT	.0750	.0009	.0296
SBTN	2.6752	.3405	.5835
SBXN 1	.1775	.0008	.0281
SBXN 2	.1592	.0002	.0129
SBXN 3	.1600	.0001	.0082
SBXN 4	.1722	.0010	.0311
SBXN 5	.2264	.0003	.0172
SBXN 6	.2161	.0007	.0269
SBXN 7	.2548	.0013	.0363
SBXN 8	.3366	.0008	.0276
SBXN 9	.3340	.0023	.0480
SBXN 10	.4528	.0009	.0299
SBXN 11	.3874	.0073	.0853
SBXN 12	.4522	.0036	.0604
SBXN 13	.5774	.0029	.0543
SBXN 14	.7754	.0100	.1002

Table I-8. Statistical Data For Brome at 80 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
MBWT	9.8869	20.0545	4.4782
MBTN	1.8607	.0416	.2041
MBXN 1	.0151	.0000	.0022
MBXN 2	.0190	.0001	.0079
MBXN 3	.0219	.0000	.0032
MBXN 4	.0151	.0000	.0035
MBXN 5	.0230	.0000	.0045
MBXN 6	.0262	.0001	.0083
MBXN 7	.0256	.0001	.0098
MBXN 8	.0438	.0002	.0145
MBXN 9	.0450	.0001	.0096
MBXN 10	.0431	.0000	.0045
MBXN 11	.0851	.0002	.0124
MBXN 12	.0899	.0007	.0255
MBXN 13	.1060	.0002	.0148



J. Statistical Summary of Ammonium Uptake Study Using  
Distilled Water



Table J-1. Statistical Data For Fescue in Distilled Water at 78 Days for Uptake of Ammonium  
Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
DFWT	1.3106	.2099	.4581
DFTN	2.1840	.2965	.5445
DFXN 1	.0301	.0000	.0063
DFXN 2	.0428	.0002	.0144
DFXN 3	.0527	.0001	.0096
DFXN 4	.0713	.0001	.0071
DFXN 5	.1355	.0014	.0380
DFXN 6	.1545	.0019	.0431
DFXN 7	.1934	.0013	.0359
DFXN 8	.2021	.0008	.0286
DFXN 9	.2065	.0024	.0488
DFXN 10	.2805	.0029	.0543
DFXN 11	.2998	.0010	.0310
DFXN 12	.3990	.0012	.0341
DFXN 13	.4458	.0031	.0557





## K. Statistical Summaries of Nitrogen Uptake by Roots and Shoots



Table K-1. Statistical Data For Brome Roots at 78 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
BMRWT	4.4630	3.6220	1.9031
BMRTN	.9821	.0240	.1549
BMRXN 1	.0680	.0041	.0637
BMRXN 2	.0775	.0019	.0432
BMRXN 3	.0942	.0025	.0496
BMRXN 4	.1061	.0019	.0433
BMRXN 5	.1299	.0005	.0219
BMRXN 6	.1576	.0002	.0124
BMRXN 7	.2626	.0056	.0750
BMRXN 8	.3246	.0033	.0572
BMRXN 9	.3604	.0005	.0226
BMRXN 10	.5065	.0054	.0733
BMRXN 11	.6005	.0238	.1543
BMRXN 12	.6451	.0135	.1161
BMRXN 13	.8284	.0297	.1723
BMRXN 14	1.1031	.0851	.2918

Table K-2. Statistical Data For Brome Shoots at 78 Days for Ammonium Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
BMSWT	9.8022	13.4633	3.6692
BMSTN	1.9582	.1119	.3345
BMSXN 1	.0125	.0000	.0035
BMSXN 2	.0099	.0000	.0008
BMSXN 3	.0108	.0000	.0014
BMSXN 4	.0075	.0000	.0059
BMSXN 5	.0089	.0000	.0044
BMSXN 6	.0124	.0000	.0006
BMSXN 7	.0132	.0000	.0018
BMSXN 8	.0133	.0000	.0033
BMSXN 9	.0289	.0003	.0172
BMSXN 10	.0269	.0001	.0075
BMSXN 11	.0230	.0000	.0048
BMSXN 12	.0277	.0000	.0038
BMSXN 13	.0418	.0000	.0038
BMSXN 14	.0768	.0001	.0103



Table K-3. Statistical Data For Brome Roots at 80 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
MBRWT	3.1386	4.8761	2.2082
MBRTN	1.0710	.0402	.2006
MBRXN 1	.0353	.0002	.0127
MBRXN 2	.0494	.0001	.0111
MBRXN 3	.0449	.0001	.0102
MBRXN 4	.0434	.0001	.0093
MBRXN 5	.0579	.0001	.0083
MBRXN 6	.0636	.0002	.0125
MBRXN 7	.0544	.0004	.0187
MBRXN 8	.0817	.0001	.0103
MBRXN 9	.1100	.0001	.0088
MBRXN 10	.1192	.0004	.0210
MBRXN 11	.1607	.0006	.0254
MBRXN 12	.1559	.0022	.0474
MBRXN 13	.1613	.0022	.0464
MBRXN 14	.2625	.0039	.0627

Table K-4. Statistical Data For Brome Shoots at 80 Days for Nitrate Uptake

Sample Weight (WT), Total N Content (TN), % Excess  $^{15}\text{N}$  Content (XN)

Treatment	Mean	Variance	Std. Dev.
MBSWT	6.7483	9.0998	3.0166
MBSTN	2.2240	.0545	.2334
MBSXN 1	.0071	.0000	.0037
MBSXN 2	.0074	.0000	.0045
MBSXN 3	.0100	.0000	.0035
MBSXN 4	.0081	.0000	.0042
MBSXN 5	.0099	.0000	.0050
MBSXN 6	.0105	.0000	.0028
MBSXN 7	.0109	.0000	.0029
MBSXN 8	.0196	.0001	.0093
MBSXN 9	.0225	.0000	.0041
MBSXN 10	.0256	.0000	.0034
MBSXN 11	.0335	.0000	.0026
MBSXN 12	.0554	.0000	.0038
MBSXN 13	.0835	.0006	.0245
MBSXN 14	.2227	.0015	.0392



L. Comparison of Constants Used in the Brome and Fescue  
Simulation Models





Table L-1. Constants Used in Brome and Fescue Simulation Models

Parameter	Brome	Fescue
KMNH4 (mol/ml)	4.12E-8	5.67E-8
KMNO3	2.565E-8	1.50E-8
VMNH4 (mg N up/g plt/h)	1.5893E-5	8.6071E-6
VMNO3	8.6071E-6	7.4643E-8
MGR (/h)	2.7936E-2	1.902E-2



M. Computer Program for Nitrogen Uptake Simulation Model by  
Brome



## Section M-1. Brome Nitrogen Uptake Simulation Model

\* SIMULATION MODEL USING CSMP III  
 \* THE FIRST SECTION IS LABELLED INITIAL AND DEFINES THE  
 \* INITIAL CONDITIONS OF THE MODEL

## INITIAL

\* UPTAKE OF NITRATE AND AMMONIUM BY MAGNA SMOOTH BROME

\* VALUES OF AMMONIUM AND NITRATE IN PPM ON BASIS OF  
 \* CONTENT IN SOIL; CONCENTRATION IN MOL/ML ON SOLUTION  
 \* BASIS

\* SOIL PPM VALUES USED: 120 PPM=2.8571E-5 MOL/ML,  
 \* 60 PPM=1.4286E-5, 30 PPM=7.1429E-6, 15 PPM=3.5714E-6,  
 \* 7.5 PPM=1.7857E-6, 3 PPM=7.1429E-7, 1 PPM=2.381E-7 MOL/ML  
 \* VALUES FOR KM, VMAX AND MAXIMUM GROWTH RATE ARE CONSTANT  
 \* THROUGHOUT THE SIMULATION  
     CONSTANT KMNH4=4.12E-8, KMNO3=2.565E-8, MGR=2.7936E-2  
     CONSTANT VMNH4=1.5893E-5, VMNO3=8.6071E-6  
 \* DATA FOR THE DOWNWARDS TRANSLOCATION OF CARBON  
     FUNCTION CTRANS=(0.0,0.4),(26.0,0.58),(30.0,0.33),...  
     (54.0,0.18),(79.0,0.153),(110.0,0.153),(120.0,1.0)  
 \* DATA FOR THE OPTIMUM RELATIONSHIP BETWEEN ROOT C/N AND  
 \* SHOOT C/N  
     FUNCTION IDEAL=(0.0,3.0),(15.0,3.0),(100.0,1.0),...  
     (120.0,1.0)  
 \* DATA FOR CHANGE IN RELATIVE GROWTH RATE WITH RESPECT  
 \* TO AGE  
     FUNCTION MAXGR=(0.0,1.0),(15.0,1.0),(26.0,.589),...  
     (46.0,.18),(71.0,.0697),(120.0,0.0)  
 \* DATA FOR CHANGE IN RELATIVE GROWTH RATE WITH RESPECT TO  
 \* SHOOT C/N RATIOS  
     FUNCTION RGRN=(0.0,1.0),(18.0,1.0),(24.0,0.9),...  
     (35.0,0.6),(50.0,0.0)  
 \* DATA FOR CHANGE IN RELATIVE UPTAKE RATE OF NITROGEN WITH  
 \* RESPECT TO ROOT C/N RATIO  
     FUNCTION RUR=(0.0,0.23),(13.8,0.23),(15.7,0.47),...  
     (18.7,0.91),(23.7,1.0),(50.0,1.0)  
 \* DATA FOR SHOOT/ROOT RATIO  
     SHRT=.184  
 \* THE INITIAL SOIL LEVELS ARE SET TO 5 PPM FOR NH4  
 \* AND 5 PPM FOR NO3  
     CNH4=1.1905E-6  
     CNO3=1.1905E-6  
     OCNH4=CNH4  
     OCNO3=CNO3  
     TOTVOL=1.0E3



\* THE FOLLOWING SECTION WILL BE EXECUTED FOLLOWING NORMAL  
 \* FORTRAN RULES AND IN THE ORDER OF STATEMENT OCCURRENCE

# NOSORT

\* INITIAL WEIGHTS ARE SET. THERE ARE TWO SETS OF WEIGHTS  
 \* USED IN THIS MODEL. WT2 REFERS TO THAT PART OF THE ROOT  
 \* WHICH IS EXPLOITING NEW ZONES OF SOIL WHERE THE CONCEN  
 \* TRATION OF NITROGEN HAS ONLY BEEN AFFECTED BY NITRIFI  
 \* CATION. WT1 REFERS TO THAT PART OF THE ROOT BEHIND WT2,  
 \* AND THE NITROGEN IN THIS ZONE IS WHAT IS REMAINING AFTER  
 \* WT2 TOOK ITS SHARE. IN THE FIRST HOUR WT1 IS ZERO AND  
 \* WT2 IS THE SEED WEIGHT. AT THE END OF EVERY HOUR  
 \* THEREAFTER, WT2 IS ADDED TO WT1.

WT1=0.0

WT2=3.5E-3

TWT=WT2

\* THE FRACTION OF AMMONIUM WHICH IS NITRIFIED

NIT=CNH4\*.0095

\* THE AMOUNT NITRIFIED IS ADDED ON

CNO3=(CNO3\*1.0)+NIT

CNH4=CNH4\*.9905

\* IN THE FIRST HOUR,

\* THE C/N RATIO OF THE WHOLE PLANT IS DEFINED

\* AND THE RELATIVE UPTAKE RATE OF N IS CALCULATED WITH  
 \* RESPECT TO THIS C/N RATIO, USING A LINEAR

\* FUNCTION GENERATOR

CNRAT=20.0

RURN=AFGEN(RUR,CNRAT)

\* MAXIMUM UPTAKE RATES FOR BOTH AMMONIUM AND NITRATE

VMAX1=VMNH4\*RURN

VMAX2=VMNO3\*RURN

\* UPTAKE IS OPERATIVE FOR .64 DAYS/DAY OR 16 HOURS/DAY

X1=IMPULS(0.0,1.0)

UT=PULSE(0.64,X1)

\* THE SHOOT/ROOT RATIO IS USED TO DETERMINE ROOT AND SHOOT  
 \* CARBON IN THE FIRST HOUR ONLY

RC=(1/(SHRT+1))\*WT2\*.45

SC=WT2\*SHRT\*.45

\* SHOOT AND ROOT N ARE CALCULATED BY DIVIDING ROOT

\* AND SHOOT

\* CARBON BY THE C/N RATIO

RN=RC\*.05

SN=SC\*.05

\* THE IDEAL RATIO BETWEEN ROOT C/N AND SHOOT C/N CHANGES

\* WITH TIME

IRAT=AFGEN(IDEAL,TIME)

\* ROOT LENGTH IS TAKEN TO BE 1,000 CM/G DRY ROOT WEIGHT OR

\* 11,000 CM/G ROOT CARBON

RL=RC\*1.1E4

\* THE VOLUME OF THE EXPLORED SOIL-ROOT CYLINDER IS ASSUMED  
 \* TO BE OF RADIUS 0.5 CM OVER THE TOTAL LENGTH OF ROOT





```

      VS=RL*.7854
* THE MOISTURE CONTENT OF THE SOIL IS HELD AT 30 PERCENT
* BY VOLUME
      VSOL=VS*.3
* THE QUANTITY OF NITROGEN (MOL)
      QNH4=CNH4*VSOL
      QNO3=CNO3*VSOL
* UPTAKE OF N IN MOLES
* CALCULATION: ((MOL/G PLANT/HR)/(MOL/ML))*(MOL/ML)*
* G PLANT*HR
      UNH4=(VMAX1/(KMNH4+CNH4))*CNH4*WT2*UT
      UNO3=(VMAX2/(KMNO3+CNO3))*CNO3*WT2*UT
* TOTAL N IN PLANT, SHOOT AND ROOT CAN BE CALCULATED
      TN=(UNH4+UNO3)*14
* THE NEW WEIGHT (2) IS ADDED TO THE OLD WEIGHT (1)
      WT1=WT1+WT2
* TOTAL WEIGHT IS CALCULATED USING THE RELATIVE GROWTH
* RATES WITH RESPECT TO AGE AND C/N RATIO
      RGRCN=AFGEN(RGRN,CNRAT)
      RGRAGE=AFGEN(MAXGR,TIME)
      TWT=TWT+(TWT*MGR*RGRCN*RGRAGE*UT)
* WT2 REPRESENTS THE AMOUNT OF NEW GROWTH
      WT2=TWT-WT1
* AT THIS POINT, THE TOTAL N TAKEN UP RESIDES IN THE ROOT
      RN=RN+TN
* CARBON TRANSLOCATED DOWNWARDS FROM THE NEW GROWTH
      FCT=AFGEN(CTRANS,TIME)
      CT=WT2*FCT*.45
*SHOOT AND ROOT C REDEFINED
      SC=(SC+WT2*.45)-CT
      RC=RC+CT
* NITROGEN TRANSLOCATED UPWARDS AND ROOT AND
* SHOOT N REDEFINED
      NT=((RN*SC*IRAT)-(SN*RC))/((SC*IRAT)+RC)
      RN=RN-NT
      SN=SN+NT
* THE CONCENTRATION OF N REMAINING IN THE
* ROOT-SOIL CYLINDER
* IS CALCULATED ALONG WITH NITRIFICATION
      RNH4=(QNH4-UNH4)/VSOL
      RNO3=(QNO3-UNO3)/VSOL
      NITR=RNH4*.0095
      RNO3=NITR+(RNO3*1.0)
      RNH4=RNH4*.9905
* THE RELATIVE GROWTH RATES WITH RESPECT TO
* SHOOT C/N RATIOS
* AND AGE ARE DEFINED AND WEIGHTS CAN BE REASSIGNED
      SCN RAT=SC/SN
      RCN RAT=RC/RN
* IN PREPARATION FOR THE FOLLOWING SIMULATION, THE
* TWO PARTS OF ROOT CARBON ARE NEEDED
      RC1=RC-CT
      RC2=CT
* THE REAL PURPOSE OF THE INITIAL SECTION HAS BEEN TO

```



\* CALCULATE THE VARIOUS PARAMETERS DURING THE FIRST HOUR.  
 \* THEY WILL NOW BE USED IN THE SIMULATION WHICH FOLLOWS AND  
 \* THE ROOT WILL BE PARTITIONED INTO THE TWO PARTS, OLD  
 \* WEIGHT, WT1, THE PREVIOUS GROWTH AND NEW WEIGHT, WT2,  
 \* THE AMOUNT OF NEW GROWTH.

\* START OF SIMULATION  
 DYNAMIC

NOSORT

\* THE FOLLOWING STATEMENTS APPLY TO THE WHOLE PLANT:

\* NITRIFICATION OF UNEXPLOITED N

NIT=CNH4\*.0095

CNO3=CNO3+NIT

CNH4=CNH4\*.9905

\* RELATIVE UPTAKE OF N WITH RESPECT TO ROOT C/N

RURN=AFGEN(RUR,RCNRAT)

VMAX1=VMNH4\*RURN

VMAX2=VMNO3\*RURN

\* UPTAKE OF 16 HOURS/DAY

X1=IMPULS(0.0,1.0)

UT=PULSE(0.64,X1)

\* THE FRACTION OF C TRANSLOCATED DOWNWARDS

FCT=AFGEN(CTRANS,TIME)

\* THE IDEAL RATIO BETWEEN SHOOT N/C AND ROOT N/C

IRAT=AFGEN(IDEAL,TIME)

\* THE FOLLOWING STATEMENTS APPLY ONLY TO THE OLD PART OF

\* THE ROOT SYSTEM, TAKING UP N IN THE REGION OF PARTIALLY

\* DEPLETED N.

\* ROOT LENGTH, VOLUME OF SOIL AND SOLUTION, QUANTITY OF N

\* REMAINING IN THAT PART OF THE ROOT ZONE AND UPTAKE

RL1=RC1\*1.1E4

VS1=RL1\*.7854

VSOL1=VS1\*.3

\* PLANT IS ONLY ALLOWED TO EXPLOIT 1,000 ML OF

\* SOIL SOLUTION OR 3,000 CC OF SOIL

IF(VSOL1.GE.1.0E3) VSOL1=1.0E3

QNH41=RNH4\*VSOL1

QNO31=RNO3\*VSOL1

UNH41=(VMAX1/(KMNH4+RNH4))\*RNH4\*WT1\*UT

UNO31=(VMAX2/(KMNO3+RNO3))\*RNO3\*WT1\*UT

\* THE UPTAKE OF N CANNOT EXCEED THE AMOUNT PRESENT

IF(UNH41.GE.QNH41) UNH41=QNH41

IF(UNO31.GE.QNO31) UNO31=QNO31

\* SIMILARILY, THE NEW PART OF THE ROOT SYSTEM IS EXAMINED,

\* GROWING INTO PREVIOUSLY UNEXPLOITED AREAS,

\* WITH N DEPLETED ONLY BY NITRIFICATION AND LEACHING.

RL2=RC2\*1.1E4



```

VS2=RL2*.7854
VSOL2=VS2*.3
IF(VSOL2.GE.1.0E3) VSOL2=1.0E3
QNH42=CNH4*VSOL2
QNO32=CNO3*VSOL2
UNH42=(VMAX1/(KMNH4+CNH4))*CNH4*WT2*UT
UNO32=(VMAX2/(KMNO3+CNO3))*CNO3*WT2*UT
* THE UPTAKE OF N CANNOT EXCEED THE AMOUNT PRESENT
IF(UNH42.GE.QNH42) UNH42=QNH42
IF(UNO32.GE.QNO32) UNO32=QNO32

* FOR THE REST OF THE DYNAMIC SECTION, THE CONTROLS ON THE
* PLANT ARE DEFINED AND ROOT N AND C/N CAN BE CALCULATED.

* THE PLANT IS ONLY ALLOWED TO EXPLOIT 1,000 ML OF SOIL
* SOLUTION OR 3,000 CC OF SOIL AT A CONSTANT WATER
* CONTENT OF 30 PERCENT
TVSOL=VSOL1+VSOL2
IF(TVSOL.GT.1.0E3) GO TO 2
RNH4=((QNH41-UNH41)+(QNH42-UNH42))/(TVSOL)
RNO3=((QNO31-UNO31)+(QNO32-UNO32))/(TVSOL)
2 CONTINUE
* N REMAINING IN THE ROOT-SOIL CYLINDER AND NITRIFICATION
NITR=RNH4*.0095
RNO3=RNO3+NITR
RNH4=RNH4*.9905
* OLD, NEW AND TOTAL WEIGHTS ARE RESET AND ARE ALSO USED
* IN THE FINAL OUTPUT
RGRCN=AFGEN(RGRN,SCNRAT)
RGRAGE=AFGEN(MAXGR,TIME)
TWT=TWT+(SC*MGR*RGRCN*RGRAGE*UT)/.45
WT1=WT1+WT2
WT2=TWT-WT1
* ROOT N COMPONENT
RN=RN+((UNH41+UNO31+UNO32+UNH42)*14)
* CARBON TRANSLOCATION DOWNWARDS
FCT=AFGEN(CTRANS,TIME)
CT=WT2*FCT*.45
SC=(SC+WT2*.45)-CT
RC=RC+CT
* NITROGEN TRANSLOCATED UPWARDS AND SHOOT AND ROOT N RESET
NT=((RN*SC*IRAT)-(SN*RC))/((SC*IRAT)+RC)
SN=SN+NT
RN=RN-NT
* SHOOT AND ROOT C/N RATIOS ARE USED WITH RELATIVE RATES
* OF GROWTH AND NITROGEN UPTAKE
SCNRAT=SC/SN
RCNRAT=RC/RN
* OLD AND NEW COMPONENTS OF ROOT C ARE RESET
RC1=RC-CT
RC2=CT
* SHOOT AND ROOT CARBONS ARE USED TO CALCULATE
* THE SHOOT/ROOT RATIO
SHRT=SC/RC

```





\* TOTAL UPTAKE AND TOTAL QUANTITY OF NITRIFICATION  
 \* IN MOLES N

TUNH4=TUNH4+UNH41+UNH42  
 TUNO3=TUNO3+UNO31+UNO32  
 QNIT=NIT\*(TOTVOL-VSOL1)  
 QNITR=NITR\*VSOL1  
 TQNIT=QNIT+QNITR+TQNIT  
 PERCN=((RN+SN)/TWT)\*100

\* WHEN THE ROOT HAS EXPLOITED 1,000 ML OF VOLUME, THE  
 \* UNEXPLOITED CONCENTRATION OF N IS REDUCED  
 \* BY THE TOTAL UPTAKE DIRECTLY

IF(TVSOL.LE.1.0E3) GO TO 1  
 TVSOL=TOTVOL  
 RNH4=OCNH4-(TQNIT/TVSOL)-(TUNH4/TVSOL)  
 RNO3=OCNO3+(TQNIT/TVSOL)-(TUNO3/TVSOL)  
 CNO3=RNO3  
 CNH4=RNH4  
 IF(CNH4.LE.0.0) CNH4=0.0  
 IF(CNO3.LE.0.0) CNO3=0.0  
 IF(RNH4.LE.0.0) RNH4=0.0  
 IF(RNO3.LE.0.0) RNO3=0.0  
 1 CONTINUE

\* THE TERMINAL SECTION SPECIFIES THE FORM OF THE OUTPUT.  
 \* IN THIS CASE, THE SIMULATION WILL RUN FOR 120 DAYS,  
 \* OUTPUT WILL BE PRINTED FOR EVERY 3RD DAY, AND 1 HOUR  
 \* IS CONSIDERED TO BE .04 DAYS (THAT IS, 25 HOURS/DAY).  
 TERMINAL

TIMER FINTIM=120, OUTDEL=3.0, DELT=.04  
 \* PRINT-PLOTS OF VARIOUS PARAMETERS. THE VARIABLE TWT IS  
 \* GRAPHED AGAINST THE INDEPENDENT VARIABLE TIME, AND THE  
 \* VALUES FOR RC, SC, AND SHRT ARE LISTED IN COLUMNS ON THE  
 \* RIGHT-HAND SIDE OF THE PRINT-PLOT, AND SO ON.

PRTPLT TWT(RC,SC,SHRT)  
 PRTPLT PERCN(RN,SN)  
 LABEL GROWTH OF SMOOTH BROME AT 5 PPM NO3 AND NH4  
 LABEL TOTAL N CONTENT OF BROME AT 5 PPM NO3 AND NH4  
 LABEL C/N RATIOS AND RELATIVE RATES  
 LABEL UPTAKE OF NH4 AND NO3 BY SMOOTH BROME

END  
 STOP  
 ENDJOB













**B30303**